The Smuts of Australia.

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THE SMUTS OF AUSTRALIA

(USTILAGINEAE).

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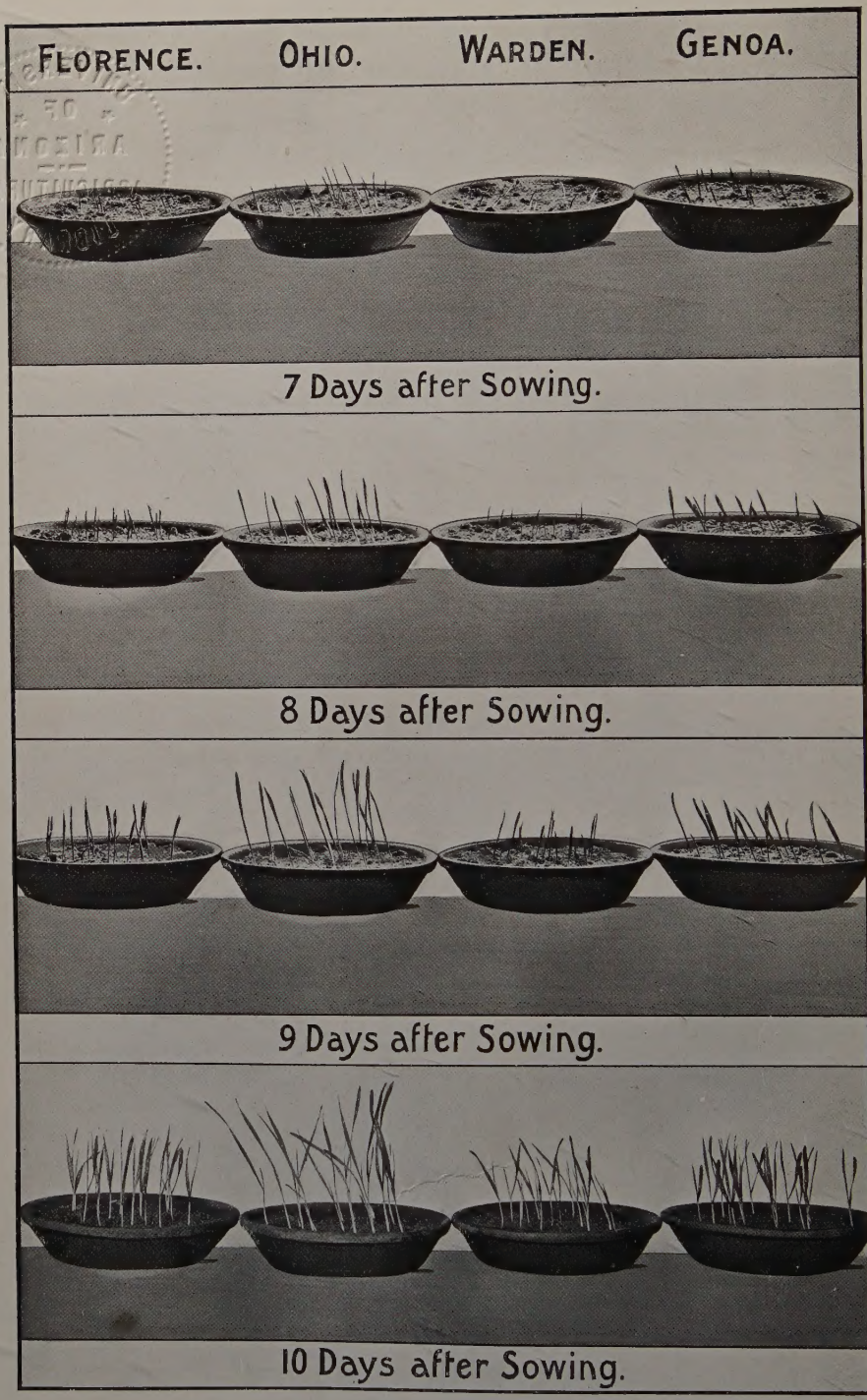

RAPIDITY OF GERMINATION
OF
VARIOUS SEED WHEATS.

DEPARTMENT OF AGRICULTURE, VICTORIA.

THE SMUTS OF AUSTRALIA

THEIR STRUCTURE, LIFE HISTORY, TREATMENT, AND CLASSIFICATION.

BY

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Government Vegetable Pathologist.

WITH 312 ILLUSTRATIONS.

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PREFACE.

This volume on the Smuts follows on the same lines as that on the Rusts of Australia, to which they are only second in importance from the amount of loss caused by them, chiefly in the cereals and grasses. Like the rusts, they are all parasitic, and have obtained the general name of Smuts from the soot-like spores which are produced in such abundance, as well as from the disagreeable odour which sometimes accompanies them.

From the plant pathologist's point of view, there is no question that these two great divisions of parasitic fungi occupy the leading position on account of the damage produced by them in cultivated crops. The diseases caused by smuts are among the most destructive, since they often destroy the grain itself which is the chief object of cultivation. From a utilitarian point of view alone, they are worthy of the most exhaustive research, in order to define them accurately so as ultimately to prevent their ruinous effects. The smut fungi and smut diseases, together with their prevention, therefore claimed next consideration to the Rusts.

It must be remembered that Australia is not as yet in the position of many of the countries of Europe and America, where the different divisions of Botany have been investigated for a considerable period by a number of trained workers. There, the systematic position of the principal groups has been more or less fully wrought out, and starting from this vantage ground, the investigator can devote his attention almost exclusively to a consideration of the conditions and results of the vital activities of the organisms he is dealing with. But in Australia the different groups of Fungi, for instance, are as yet very imperfectly known, and we have still to classify and accurately describe many of them.

Hence I consider the first duty of the investigator of these diverse organisms in Australia is to fix their position in the general scheme of plant-life and *then* to identify special structural features with particular physiological functions; in other words, to determine their life-histories as completely as possible. No doubt the knowledge thus acquired will be reflected in and possibly modify our classification; still, to give definiteness to our researches, the species investigated should be clearly defined.

The object of the present work, then, is to classify and describe all the known species of Australian smuts, to supply photomicrographs of their spores and other important features so as to fix their identity, and to give an account of their life-history as far as present knowledge goes, in order that a rational mode of treatment may be adopted for preventing their ravages in our cultivated crops.

Besides, the photomicrographs of the different species will always mark out their individuality, no matter what position may be assigned to them in any future scheme of classification. In a review of my previous work on *The Rusts of Australia*, it was remarked that "There are far too many photomicrographs; a few give verisimilitude to a paper and confirm the *bona*

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fides of the author, but good hand-drawings are always better for reference, if they can be relied on." Notwithstanding this criticism, the present work proceeds largely on the same lines, for the unquestioned fidelity to nature which photomicrographs represent, far outweighs the seeming clearness and explicitness of an ordinary drawing. It is really astonishing to find how often scientific error is perpetuated, because it is based on drawings of what the author imagined but did not really see.

I have to acknowledge the valuable aid given by my former Assistant, Mr. G. H. Robinson, and my present Assistant, Mr. C. C. Brittlebank, as the various photomicrographs executed by them show strikingly the essential features of the different species.

To all who have generously supplied specimens and copies of their papers relating to the subject, I tender my sincere thanks. I am specially indebted to Professor Ewart, Government Botanist, who allowed me free access to the National Herbarium, and to the Director of the Royal Gardens, Kew, who readily placed at my disposal such specimens as were available only at that institution. My colleague, Mr. C. French, Government Entomologist, and his Assistant, Mr. C. French, junior, have been indefatigable in securing specimens, and noting the distribution of these harmful parasites.

It is hoped that the work may prove useful in the education of the farmer, who is now becoming alive to the necessity of knowing the nature of the pests which devastate his crops, for it is mainly by the knowledge of the habits of the parasites which cause the disease that disease prevention can be secured.

Not only to the man on the land does this work appeal, but now that Agricultural High Schools and Colleges are established in most of the States and a Chair of Agriculture has been founded in Sydney University, the diseases of plants should become a recognised subject of study at all such institutions. It is beginning to dawn on the minds of our legislators that the importation of pests must be stopped, so that a Quarantine Act has been passed, and it is only a step further to realize that the spread of disease within the States must also be checked. All this legislation will demand increased knowledge on the part of those who have to administer such Acts.

Attention is frequently called to the small average yield of wheat produced by the Commonwealth—10½ bushels to the acre—and how to raise it is often discussed. While careful cultivation, suitable rotation, and judicious manuring will all tend in that direction, it is hardly ever thought worthy of mention that the ravages from various preventable diseases are responsible for a considerable amount of the annual shortage.

With irrigation and intense culture, it is soon discovered that the sunshine and the water, which promote the growth of our cultivated plants, favour their parasites as well, and thus the study of Vegetable Pathology is becoming more and more a matter of national importance, and must soon cease to be, as it is at present, a neglected department of knowledge, if the industrious settler is to reap the full reward of his labours.

Melbourne, April, 1910.

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I.

GENERAL CHARACTERS.

CHAPTER I.

Introduction.

Every farmer is more or less familiar with the ordinary smuts, which are so frequently seen in our cereal crops, either converting their ears into a sooty mass, or indicating by their fœtid odours, especially when crushed, the presence of a disagreeable and destructive parasite. But they are by no means confined to these hosts, for they are very common on grasses generally and occur on a number of flowering plants. Only one smut has been found outside of this group, on the capsule of a Sphagnum, or peat-moss. It is in reality only the spores which appear on the surface, as the body of the plant which produces them is deeply seated in the tissues. The spores are formed in all the different organs of the plant, generally where food material is most plentiful, but usually are confined to one definite position, which is characteristic for the species. The grains and seeds are favourite spots for the development of the spores, since the supply of food is not only abundant and choice, but they are also in such an exposed position that they are readily distributed. They reach the healthy grain in various ways, and there is an evident advantage in being carried and sown with the seed. One would hardly expect to find smut spores produced at the collar of woody trees, but, according to Vuillemin[1], this is the case with at least one species which produces woody tumours on Eucalypts. The species which is known as *Ustilago vriesiana* occurred in the Botanic Garden, Amsterdam, on various species of Eucalypts, including *E. globulus*, *E. amygdalina*, *E. rostrata*, *E. leucoxylon*, and *E. macrorrhyncha* and there is every probability that it exists in Australia, although hitherto overlooked. It is the only Ustilagine known to produce a woody tumour, and its spores, formed in cavities between the wood and the bark, are described as violet-brown, oval, smooth, measuring 7–9 × 5–7 μ. In one of the smuts attacking maize the spores may be produced on the adventitious roots above ground, stems, leaves, or inflorescence and the Flag Smut of wheat, as the name indicates, is usually confined to the leaves. Even the anthers of the flower may be invaded by a smut, as in the case of the Carnation and other species of that family, where the spores of the smut replace the pollen of the flower and are discharged just like the pollen.

The smut, as is the case with other parasites, may stimulate the part attacked and cause an abnormal growth, so that the plant endeavours to meet the extra demands made upon it by the fungus. The smut-boils of the Maize are well-known examples, and it is interesting to note that they contain probably the same alkaloid as the Ergot, and the fluid extract is used in a similar manner. Not only is there a smut used in medicine, but there is one used for food, viz., *Ustilago esculenta*, P. Henn. Only the upper extremity of the shoot of *Zizania* is smutted, and the swollen and deformed portion is eaten in China as a vegetable.

Wherever the spores are produced they are in such countless numbers that a supply for next season is usually assured, and if the conditions are favorable for their germination at the proper time, infection as a rule occurs, and the smut is propagated.

The infection tube can only penetrate the host-plant and become parasitic at a spot where the tissue is young and tender. This may be in the young seedling, leaf, or stem, but it may also occur in the flowering stage when the young ovary is just forming.

If we follow the spore of the Stinking Smut of wheat from the time it is shed until it reaches a fresh plant next season, the way in which the disease is carried from season to season will be evident. In a district where this smut occurs, the sound grain may receive the spores by means of the wind or in the threshing machine, and this seed with the adhering spores may be sown in the same or in another district and thus introduce the disease. The grain in due course germinates, and the self-same conditions which are favorable to the germination of the wheat also suit the smut spores. They readily germinate with moisture and produce secondary spores, or conidia, which in turn put forth delicate threads, and these readily enter the young wheat seedling. There they soon reach the growing point of the stem and continue to grow, plant and parasite being supplied with food from the same source. Under ordinary conditions of growth the wheat-plant is able to provide sufficient food material for both, and this goes on until the flower is formed and the young ovary begins to develop. Then the plant ceases to manufacture fresh material and transfers what has already been accumulated to the grain, for the benefit of the young and growing embryo. Here the fungus luxuriates in the rich supply of food and the filaments increase, multiply, and divide into innumerable branches, from each of which spores are formed; the wall of the filaments becoming gelatinous. The wall soon deliquesces and is absorbed by the growing spore, which soon assumes its firm black covering; and what was at first intended as a store-house of nourishment for the embryo has been converted into a charnel house, densely packed with the spores of the overmastering fungus. These spores again reach the sound grain and repeat the process in the succeeding crop. The principle on which the treatment for the prevention of this smut is based, may be clearly seen from this brief account, for if the spores on the grain are destroyed, or their germinating power arrested, they will not be able to infect the young seedling and produce the disease.

The losses caused by this smut are enormous, and these are not only due to the actual reduction in the yield of grain, but to the indirect loss brought about by the sound grain having its commercial value lessened from the adhering spores of smut, which are easily recognised by their objectionable smell. It was estimated, from reliable data, that in one season this State suffered a loss of £50,000, although in recent years the general treatment of the seed-wheat has reduced considerably this preventable loss. Even the loss from Loose Smut of wheat is considerable, although the farmer does not always allow for it, and may even blame something else for the naked stalks throughout his crop. In South Australia, it is considered that in some seasons more damage is done to wheat by Flag Smut than even by the dreaded Rust, and in certain districts of Victoria the yields are much reduced from that cause alone.

In the countries of the Old World, the loss due to smut is regarded as only surpassed by that caused by Rust, and in the United States, Swingle[2] has calculated the yearly loss from Oat Smut to amount to £3,600,000, and for the State of Ohio alone, Selby[2] has reckoned the Stinking Smut of wheat to cause a loss of £50,000. For both these diseases a remedy has been provided, and it lies with farmers themselves to take advantage of it.

Historical.—While the mildew or rust of wheat is freely mentioned by ancient writers, the smut of wheat is not specially noticed, and there is no word to express it in the language of Greece or Italy. Pliny speaks of the blasting of corn "which cometh of some distemper of the air," but this, in all likelihood, refers to Rust, for he goes on to remark "this unhappy blast falleth most often in places subject to mists and dews, such as hollow valleys and low grounds." It does not necessarily follow, however, that it was not

known in ancient times, for the probabilities are that it was included under the general term of mildew or blight. Thus, Bacon says, "Mildew falleth upon corn and smutteth it," and even now, Rust and Smut are often confounded, the name of "Black Rust" having been applied to Flag Smut for a number of years in South Australia.

In historical times, the nature and origin of smut were much discussed, and the different views held by eminent writers brought it prominently into notice. The Stinking Smut of wheat was evidently the first to attract attention, for Tull, writing in 1733, remarks that "Smuttiness is when the grains of wheat, instead of flour, are full of a black stinking powder." Then, in 1755, Tillet distinguished between *la Carie* the Stinking Smut, and *la Charbon* or Loose Smut. The grains composing the smut were supposed to resemble the spores of puff-balls, and being enclosed by the walls of the ovary, Bjerkander[1] classified this form as a *Lycoperdon*, in 1775. But this view was not generally accepted, and Tessier, in 1783, while acknowledging the resemblance to *Lycoperdon*, considered it rather as a degeneration of the grain and not a definite and independent organism. He, along with others, had observed that the powder was contagious, but did not know how that powder originated. In seeking to account for it all sorts of wild notions were entertained. Some regarded the black particles as foreign bodies, others as infusoria, and still others considered them as indications of an offended deity, for in an article on the subject of smut, in the fifth volume published by the Bath Agricultural Society, in 1790, the following occurs :—"Premiums, offered for preventing evils which originate from intemperate seasons and destroying blights, may excite invention, artifice, cuming, imposture, and deception, but can never extend the boundary or expand the circle of human knowledge or human power. He, and He only, who can repel the malignant blasts of the East; fraught with myriads of consuming insects, which originate from what or where none but Omniscience knows, and substitute the soft, healing, balmy zephyrs of the West, can reward the labours of the industrious husbandman with plenty and happiness."

But the view of the smut as being due to degeneration of the plant itself persisted for a long time, and was held by eminent scientists. Instead of regarding the smut powder as consisting of spores capable of reproducing the fungus from which they were derived, they were considered to be diseased outgrowths, morbid conditions, or eruptions of vegetable matter. As late as 1833, this was the view put forth by such a good observer as Unger, in his work "Die exantheme der Pflanzen" and it was adopted by Schleiden even in 1846. About a century ago, in 1807, Prevost[1] discovered the important fact that the smut spores germinated in water, and consequently showed that the smuts were of the nature of fungi. Unger, in referring to this, remarks that, although fungus filaments were produced, there was no evidence to show that they possessed the power of infection. This evidence was only forthcoming in 1858, when Kuehn directly followed the penetration of the germ threads in wheat.

With our present knowledge, it seems difficult to conceive that even when the smuts were acknowledged to be fungi, and that they produced spores, it should still be maintained that they were of the nature of diseased outgrowths from the plant itself. The facts of their development were generally known; but that the spores were capable of infection had still to be experimentally proved. Even such a distinguished physiologist as Meyen[1], in 1837, did not realize the importance of the spores in the production of the disease, although he described their formation accurately as shown in the following passage :—"I consider it to be an established fact, that the smut (*Ustilago*, Link) is not a contagious disease, but is inherited, and arises from the stoppage of the saps

produced by superabundant manure foreign to the nature of the plant. At one or at several places of the inner surface of the affected cells, small deposits of mucus are formed from which filiform ramified bodies proceed, which are colourless and almost transparent, but contain a quantity of small molecules consisting of a somewhat more solid substance. These mucous filaments, in the interior of the cells, soon present constrictions at various places, first generally at the apices of the small lateral branches; and these constricted ends take an ellipsoidal and lastly, a spherical form, become of a yellow colour, and change into those minute brown vesicles of which the smut consists. The destruction of the cellular walls by dissolution commences with the aggregation of these smut vesicles in the diseased cells, and then these vesicles are found in great masses lying close together, filling entirely the diseased organ, and frequently without leaving a trace of the original intervening cellular wall." It is still deeply rooted in the minds of many farmers that the smut spores are simply an exudation of the sap of the plant, blackened by exposure to the air, or that the fungus, if fungus it be, has arisen spontaneously from the soil in some mysterious fashion. It is only when the spores are seen to germinate, and when the infected grain produces smutted plants, while those produced alongside free from spores are perfectly healthy, that the fungus is realized to be a parasite, the presence of which is necessary for the production of the disease.

The next step in advance was by Tulasne[1], in 1847, who investigated methodically the germination of the spores in water, and proved that on germination they did not directly give rise to a mycelium, but to a short germinal tube which produced minute reproductive bodies. He distinguished the germinal tube as a promycelium, and the reproductive bodies as sporidia, and having a somewhat similar mode of germination to the teleutospores of the rusts, he came to the conclusion that the rusts and the smuts were closely allied. Next, Kuehn[1], in 1858, carried out infection experiments with the spores on various host-plants, and he found that the fully developed plants were not capable of infection, but only when they were in the seedling stage. The production of sporidia, as shown by Tulasne, and the mode of infection of the host-plant as demonstrated by Kuehn, gave a simple explanation of the development of the smut, and seemed to account completely for all the observed phenomena. When one considers how intimately the smut fungus is associated with its host, how it enters the young seedling and goes on growing within the tissues of the apparently healthy plant, how it suddenly appears in the ovary and replaces the floury contents of the grain with the black smutty spores, it is not to be wondered at that it was regarded at one time as part and parcel of the plant itself.

The mode in which the spores are formed next engaged attention, and De Bary[1], as early as 1853, extended our knowledge in this direction. Fischer von Waldheim[1] also carried on his investigations into the germination of the spores and the mode of their formation. But it was only when Brefeld began his masterly and epoch-making researches into the germination of the spores of the various smut fungi in nutrient solutions that the subject was dealt with in a thorough and complete manner. This was in 1883, when the first part of *Die Brandpilze* was published, and there he showed that it is only by rigorously following exact scientific methods that the boundaries of knowledge can be enlarged. He found that the germination of the spore in water was often uncertain, slow, and in some cases, such as Maize Smut, it was difficult to secure it at all. He therefore hit upon the happy expedient of germinating the spores in nutritive solutions, such as a watery extract of manure, or of such vegetable substances as are contained in the soil. In the fluid extracts of such materials, not only did the spores germinate as in water, but even

spores which would not germinate at all did so without exception. It was further discovered that the germination went beyond that which occurred in water and was not only more luxuriant, but that instead of stopping at that stage, the secondary spores or conidia began to sprout on their own account. These *sprouting conidia* as they are called by Brefeld, continued to multiply indefinitely as long as the nutrient material lasted, and, becoming detached, continued the process just like yeast-cells. Some of these sprouting conidia had also the capacity of giving rise to *aerial conidia*, which, on account of their minuteness, were scattered in immense numbers by the wind. The final step was taken when infection was proved to take place, not only in the seedling, as in Stinking Smut of wheat, but also in the young and tender tissue of developing maize plants as in the American Corn Smut, and in some cases, in the flower itself. This floral infection was first practically demonstrated and described in 1896, by Maddox, in the *Tasmanian Agricultural Gazette*, and afterwards re-discovered, in 1905, by Brefeld.[7] The probabilities are, that some host-plants are capable of infection both through the young seedling and the flower, but that has yet to be proved.

Hitherto, it was taken for granted that the parasitic fungi could only live and grow upon the particular host-plants with which they were associated in nature, and that it was only by confining observations and experiments to the host-plants that the full course of their development could be traced. But Brefeld opened up a new field of inquiry when he showed, in the most convincing manner, that parasitic fungi can live outside of the host-plant, and that in nutrient solutions they could grow as luxuriantly and sometimes even more so than they did on their natural hosts. While the smuts can maintain themselves on the living plant, they are also capable of existing on dead organic substances, and thus the line of demarcation between parasites and saprophytes was shown to be less rigid than commonly supposed. In fact, there are sources of infection quite outside the host-plant which have to be taken into account when considering the propagation and prevention of smut.

Each successive step in advance has thrown fresh light upon what takes place in nature, and the discovery of infection through the flower has explained how it is that in Loose Smut of wheat, and Naked Smut of barley, disinfection of the seed has not been successful in preventing the disease, and how the smut may break out in places where it has never before been known, through being carried in a dormant condition within the seed, even although that seed had been carefully treated and there were no wild or cultivated grasses in the neighbourhood from which it might have been derived.

[*To face Plate I.*]

MYCELIUM.

(*a*, *b*, after Plowright; *c*, after Fischer von Waldheim.)

a. *Ustilago avenae* .. Hypha from axis of inflorescence of Avena elatior .. ×500
b. ,, ,, .. Hypha gelatinized from same plant .. ×500
c. *Tilletia striaeformis* .. Hypha from leaf with large vacuoles and showing double contour in walls .. .. .. ×900

SPORE FORMATION.

(*d*, after Brefeld*; *e*–*k*, after Fischer von Waldheim.)

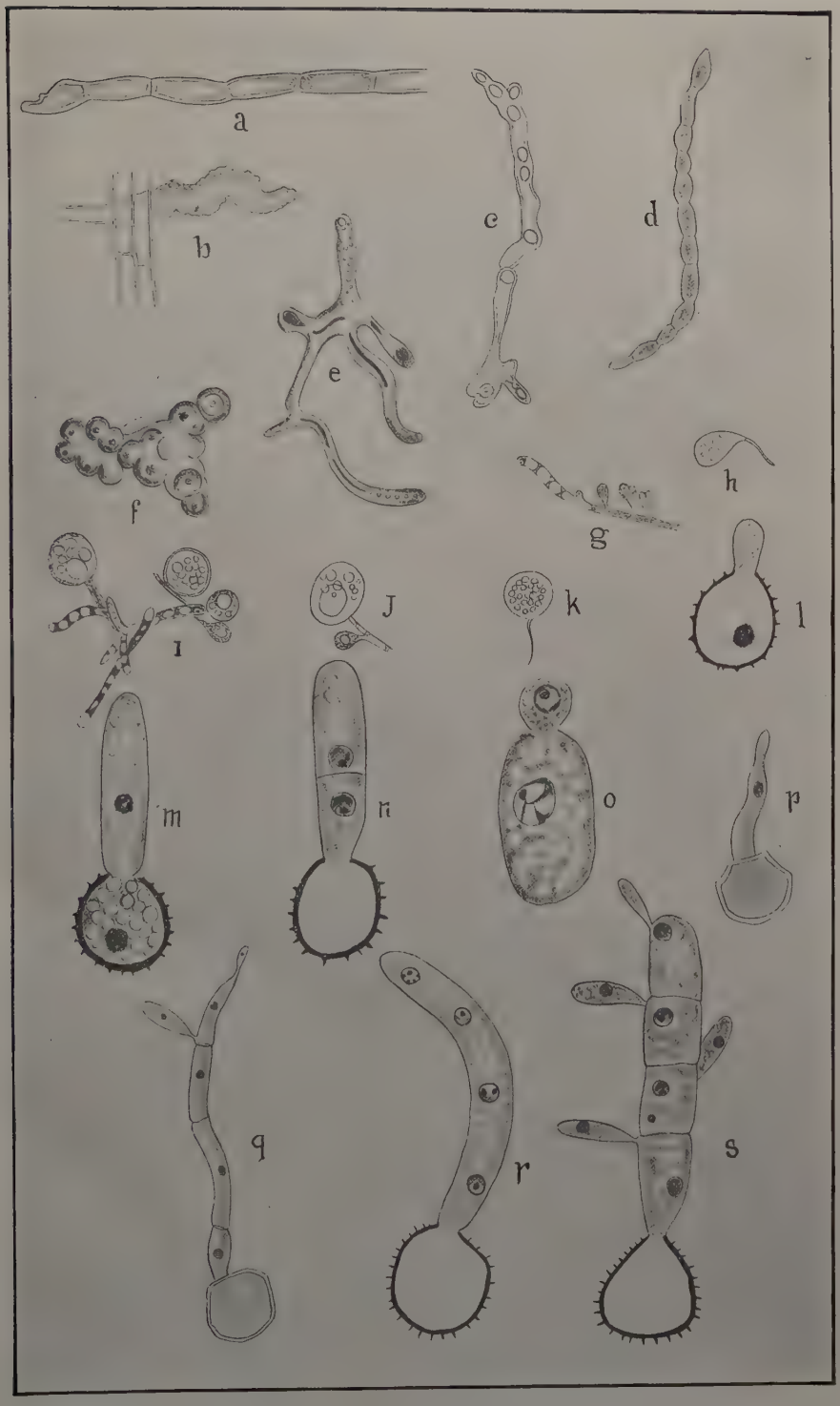
d. *Ustilago olivacea* .. Spore-bearing hypha, the swellings indicating the formation of spores .. .. ×400
e. *Ustilago zeae* .. Gelatinized hypha showing the contents breaking up for spore formation .. .. .. ×900
f. *Ustilago violacea* .. Coalesced gelatinous hyphae in which spore formation is taking place, and contour of spores distinctly visible .. .. ×900
g. *Tilletia levis* .. Spore-forming hypha with commencement of branches ending in spores .. .. ×900
h. ,, ,, .. Young spore still connected with hypha .. .. ×900
i. ,, ,, .. Young spores in various stages of development .. ×500
j. ,, ,, .. Separation of hypha into two branches with spore at end of each of different degrees of ripeness .. ×500
k. ,, ,, .. Spore with shrivelled remains of spore-forming hypha ×500

SPORE GERMINATION.

(*l*–*o*, and *r*–*s*, after Harper; *p*, *q*, after Istvanffi.)

l. *Ustilago violacea* .. Germinating spore with nucleus .. .. × about 1500
m. ,, ,, .. Germinating spore after first nuclear division, one nucleus remaining in spore, the other wandering into germ-tube .. .. .. × about 1500
n. ,, ,, .. Promycelium, with two daughter nuclei and a septum between .. .. × about 1500
o. ,, ,, .. Conidium budding like yeast .. .. × about 1500
p. *Ustilago maydis* .. Germinating spore with single nucleus in promycelium .. .. ×950
q. .. Four-celled promycelium and conidia with a nucleus in each .. .. ×950
r. *Ustilago scabiosa* .. Promycelium with four resting nuclei .. × about 1500
s. ,, ,, .. Four-celled promycelium and conidia with a nucleus in each .. .. × about 1500

* The magnification of Brefeld's figures is generally too high, probably arising from the mode of reproducing them.



G. H. Robinson, Phot.

MYCELIUM, SPORE FORMATION AND GERMINATION.

CHAPTER II.

Vegetative Organs—Mycelium.

Among parasitic fungi, such as the smuts, it is by means of the mycelium that they obtain their nourishment from the plants on which they prey, and it is therefore the vegetative part of the parasite. Hence, although hidden in the interior of the tissues, it is the foundation of all the disease and deformation which afterwards occur. It is not of itself an evident cause of disease in the plant, for it is generally so intimately bound up with the host-plant and grows so regularly with it, that there is usually no external evidence of its presence. It is only when the spores are formed that the fungus is revealed, and then what remains of it is often used up in their production, so that there is no portion of the fungus which is more easily overlooked or less seldom investigated than the mycelium. Commencing in the young seedling, as it generally does, and growing steadily with it until the seed again is formed, it can readily be understood that the fungus filaments are difficult to detect among the tissues. They are most easily seen in the vicinity of the spore-beds, but even in the early stages of their formation they can be detected, as in the neighbourhood of the growing point of cereal seedlings.

The mycelium is composed of hyaline tubes, which are usually septate, copiously branched and comparatively narrow, being only on an average about 2–5 μ broad (Plate I., *a*, *b*). The walls of the hyphæ are relatively thick, and sometimes a decided double contour of the membrane is visible (Plate I., *c*). When treated with iodine and sulphuric acid or chlor-zinc-iodine there is no blue colouration produced, showing that they are not composed of cellulose. From the transparent nature of the walls and the watery contents of the cells, often filled with vacuoles, it is necessary to use reagents to make the mycelium stand out clearly from the surrounding tissue. If the tissue of the host-plant containing mycelium is kept in a strong solution of potash for 24 hours, the fungus filaments are rendered more distinct in contrast with the clear and transparent tissue surrounding them. The hyphae not only ramify between the cells of the host-plant, but may even penetrate into them and form haustoria, which are seldom spherical, but most frequently like a bunch of grapes. In the cereals, long unbranched hyphæ are mostly found in the internodes, while in the nodes they are much branched and convoluted.

Perennial Mycelium.

In the Rusts, the mycelium may either confine itself to definite spots and become localized, or it may permeate the entire plant, or at least large portions of it. In the Smuts there is a similar arrangement. When the young ovary is infected as in the Loose smut of wheat (*Ustilago tritici*), the mycelium is restricted at first to that portion of the host-plant, but in most cases the seedling is attacked, and then the mycelium permeates the entire plant. When the spores are being formed, it is most readily found in their vicinity, but it originally existed throughout the plant, although the earlier formed portions may have disappeared. The mycelium persists more particularly in the nodes, where it remains dormant, but if the host-plant is perennial and gives rise to fresh shoots next spring, it awakens into fresh life, and enters the new growth, as in *Ustilago perennans*, Rostr.

I had a very good illustration of this in the case of a barley plant affected with Naked smut (*Ustilago nuda*). It is commonly stated that the stubble of wheat and barley will not sprout again, because the original forms are annual; but under our conditions with the ripening season in the summer, and not in the autumn, they may be cut back while still somewhat green and shoot again, and behave as if biennial. This occurred in a plot of Battledore barley sown at Burnley on 2nd July. The ears in one plant were all smutted with the Naked smut, and this smutted stool was cut close to the ground on 6th November, before it was dead ripe, in order to encourage a new growth. The season was favorable and a second growth started, and by the 24th December fresh ears were formed, which were also all smutted, as in the first instance. In this case when the plant was cut down, the mycelium still remained alive in the basal portion, particularly in the nodes, and when fresh shoots were formed later on, the mycelium entered into them and produced the disease. Sections of the lowest node revealed the presence of fungus filaments, so that it was not by shoot infection, but from the perennial mycelium that the fungus arose.

Not only may a cereal crop be cut once and shoot up again, but it may even do so a second time. In Victoria this happened with a crop of oats. The land was ploughed and sown in October, 1907, and about 10 acres were sown with Algerian oats. The crop was cut in January, 1908, and yielded about 25 cwt. to the acre. Then heavy rain set in and the crop was cut again in April, yielding hay of splendid quality, and averaging 1 ton per acre. The paddock was heavily stocked from April to October, when it was again closed to stock, and the third cutting taken off in December, 1908. This was the heaviest crop of all, and yielded about 30 cwt. per acre. The land was open plain country, at an elevation of 3,500 feet above sea level. If smut had been originally present in the crop it would probably have appeared in each successive cutting.

Although the mycelium may thus permeate the entire plant, it is only at certain definite spots where spore-formation occurs. In the case of *Tilletia tritici*, however, Berkeley[1] has recorded an instance where a streak of the smut spores appeared on the outside of the stem, thus showing that, while the normal appearance of the spores is in the grain, they may be produced in the stem under rare conditions. I have also observed in *Ustilago tritici* that, while the spores are usually produced in the spikelets, they may occasionally occur in elongated streaks on the sheathing blade or shot blade enveloping the ear in its earliest stages, as well as on the stem (Plate VI., *c*)

Localized Mycelium.

It frequently happens that where the mycelium is confined, it gives rise to swellings known as smut-balls or smut-galls, varying from the size of a pin-head to that of a child's head. These swellings in the American Corn smut, for instance, are not merely due to the multiplication of the fungus filaments, but also to the luxuriant growth of the tissues of the host-plant. The Gall smut of Barnyard grass may give rise to elongated swellings, reaching a length of 9 cm. (Plate XXI.).

The mycelium is generally hidden in the tissues of the host-plant, but it sometimes forms a fungus membrane on the outside. This only occurs, however, in connexion with, and as a protective covering for, the spores until they are ready for distribution.

CHAPTER III.

Reproductive Organs—Spores.

Just as in the Rusts, the spores form the most prominent feature and play a most important part in the determination of the species. Hence they have received a large share of attention at the hands of investigators, and will require to be carefully studied in their various bearings. There is a good deal of confusion in the use of the term spore, since it may be applied in a general way to all the reproductive bodies of these fungi, and in order to fix definitely the exact position it occupies in the course of the life-history a qualifying word is often prefixed to it. We refer to the spores which arise in the form of a dark powder, and to which the familiar name of smut or bunt is given.

Since the spore and its products are constantly being referred to, the terms generally employed to designate them may be appropriately given here, indicating at the same time those which will be commonly adopted in describing the life-histories of the various species. As members of the great group of Fungi, the smuts have necessarily much in common in their vegetative and reproductive processes with the others, and there are consequently general terms which are applicable to all, but, on the other hand, there are special characters which distinguish them from the others, and to express these distinctions special terms have been employed. The names given will vary according to the different views held as to their relationships, and they will presuppose affinities which may, or may not, be borne out by facts. The following scheme shows at a glance the various names given to the spore and its products by prominent investigators of this particular group :—

General terms—Spore=	Germinal Tube=	Conidium=
Special terms—	Promycelium (Tulasne and De Bary)	Sporidium (De Bary)
Resting-spore (De Bary)		Conidium (Brefeld)
Chlamydospore (Brefeld)	Hemibasidium (Brefeld)	Sporidiolum (Saccardo)
Teleutospore (Plowright)		Promycelial spore (Tulasne)

As regards the spore itself, De Bary calls it a resting-spore, because it usually undergoes a period of rest before germination, and Brefeld speaks of it as a chlamydospore, on account of its firm membrane, while Plowright regards it as a teleutospore, being the supposed equivalent of that spore in the Uredineæ. Amid all this diversity of naming we will simply call it a *Spore*, as it is the main reproductive body, and the other spore-like bodies derived from it will receive special designations.

The spore on germination produces one or more germinal tubes of the nature of a hypha. This hypha may either elongate, branch, and become the foundation of the mycelium, or, as in the Rusts and Smuts, it may be very limited in its growth, and give rise directly to other spore-like bodies unlike the mother-spore, and then die off. On account of this special feature of the product of germination in the Rusts, Tulasne called it a *Promycelium*, because it represented a mycelium in a very abbreviated form, and because a similar short and short-lived germinal tube was produced in the Smuts, De Bary likewise gave it the name of promycelium. But Brefeld introduced the term hemibasidium to indicate the relationship which he considered to exist between the Ustilagineæ and the Basidiomycetes. The name of promycelium, however, is distinctive without involving any particular view of relationship, and will be adopted here (Plate I., *l-s*).

The germinal tube or promycelium (by a process of abstriction) proceeds directly to the formation of reproductive bodies, which differ in no essential particular from the *Conidia* similarly produced in other groups, and Brefeld has adopted that term. But De Bary uses the name sporidium as originally proposed by Tulasne for the promycelial spore in the Rusts, and considering that the term had already been used for the ascospore in the Ascomycetes, and Saccardo had therefore altered it to sporidiola, it will avoid the unnecessary multiplication of terms to retain the old name of Conidium (Plate I., *q*, *s*).

The typical description of the mode of germination will therefore be that the spore produces its short germinal tube or promycelium, which in turn gives rise to conidia, and there may be secondary and tertiary conidia produced, or even those which sprout in a yeast-like manner, and are therefore called sprouting conidia. Although I have adopted here, for the sake of simplicity, the term conidium for the product of the promycelium, it is not to be regarded as necessarily different from the similar body produced in the Rusts, for which the name of Sporidiolum was chosen.

Structure.

The spores are colourless at first, and gradually assume a brown or black colour, which is confined to the outer thick membrane or *exospore*, while the inner or *endospore* is thin and remains colourless. The exospore is not only coloured and thickened, but its surface may be either smooth or roughened in various ways. It may develop spines, warts, or net-like markings, but sometimes the markings are so minute as to be simply granular.

The spores are either free, as in *Ustilago*, or united into spore-masses, as in *Sorosporium*. This formation of spore-clusters is brought about by the sporogenous hyphæ becoming densely interwoven, and when the spores are subsequently formed they grow together, and so remain united in heaps. If they are not thus firmly united, the spores may occur in clusters, and yet be easily separated, so that they belong to the free-spored forms. The division to which they belong can only be definitely settled by tracing their development and mode of formation, unless when they are permanently and not merely temporarily united. It can readily be understood that there is no great morphological difference between the forms with free and with united spores, and even in the germination of the individual spores there is considerable resemblance. But the distinction is well marked where the spores of a cluster have a special envelope consisting of sterile cells, as in *Urocystis*. These outer sterile cells not only protect the fertile inner cells, but probably serve as floats to carry them to a suitable place for germination. The protection to the spores has reached its highest development in *Doassansia*, where the clusters of spores are enclosed in a highly specialized peridium, consisting of densely packed sterile cells, reminding one of the protective cells in the Gasteromycetes, and there known as a peridium. The spores thus protected are able to remain under water for a considerable time, and they may germinate either under water or on damp earth by the germinal tube bursting through the envelope.

Dispersion of Spores.

As in the great majority of fungi, the wind is the most important agent in distributing the spores. When the smut is produced in the ear or inflorescence, as it generally is in grasses, it is in a favorable position for the wind to play upon it, and the gentle swaying to and fro of the plants will help to shake out the spores even in a still atmosphere. The spores thus distributed may fall upon the ground, or be carried to healthy grains where they attach themselves to the surface, as any small particles of dust might

do, and in this way may convey the disease to great distances from its original source. The conditions favorable for the germination of the grain are those most suitable for the germination of the spore, and it is, generally speaking, the best time for the infection of the young seedling as well.

In the case of Flag smut of rye or wheat, while a proportion of the spores may be blown about by the wind, the greater number remain attached to the leaf, and when this withers up and falls away and becomes torn into shreds, it not only forms a convenient means of dispersal, but preserves the spores in the soil until the next season, when they can infect the seedling plant. The examination of commercial samples of wheaten chaff from various parts of the State and the detection of spores of this smut in greater or less quantity, show that this is a very efficient means of dispersion.

Thaxter[1] regards it as very probable that insects may serve to spread the spores, as in some other fungi, for he notes that the smut of Onions (*Urocystis cepulae*) appears to be attractive to the "flea beetles," which swarm over the diseased seedlings, and apparently feed upon the spores, while they do not seem to visit the healthy onion leaf.

Brefeld[2] has observed that in some species the spores separate from one another in water with a sort of jerk, as if some sort of intermediate substance pressed them asunder, as in *Cintractia spinificis*, (Ludw.) McAlp. Probably swelling of the membrane, which occurs in spore-formation, also subsequently plays a part in spore distribution, but it may also be that the mycelium left over after the formation of the spores retains the capacity for swelling.

Spore Formation.

The spores are not formed from the ordinary mycelium, but at those spots where the spores arise, the vegetative mycelium gives rise to special spore-bearing filaments. These filaments are produced directly as branches which are quite distinct in their appearance and behaviour (Plate I., *g-k*).

In connexion with the various genera, it is not only necessary to determine the nature of the spores, but also the mode of their formation, for it is only by means of such characters that the genera can be properly distinguished. Hence it follows that each genus will require to be dealt with separately, but a general view of the process may here be given.

The spore-forming filaments have their walls swollen in a gelatinous manner, and contain a granular protoplasm in which a number of oleaginous particles are often seen. This gelatinization of the walls of the filaments is a fairly constant character, but it does not occur in every species (Plate I., *e, f*).

The ordinary mycelium may change quite suddenly into the spore-forming, as in *Sorosporium saponariae*, or it may be more gradual as in *Ustilago longissima*, where the extremity of a filament may show the gradual gelatinization and spore formation.

When a filament is preparing for the process of spore-formation, its walls become distended, while its cavity is diminished. Then the whole enlarges together with the lumen, and the protoplasmic contents are ready to be transformed into spores (Plate I., *d*).

The spore is regarded by some authors as the result of a sexual process, and it will be convenient to consider here the question of sexuality as occurring in the Smuts. The evidence of sexuality is based upon the behaviour of the nuclei, the presence of which is now firmly established in the smuts, and not only so, but these nuclei are shown by Harper[1] and others to possess the same essential differentiations in structure that are met with in the higher plants (Plate I., *l-s*).

Dangeard[2] found that the young cells of the mycelium or vegetative cells contain two nuclei, although older cells may contain more than two. Then when spores are about to be formed, this formation occurs in special swollen cells, each of which contains two nuclei, as in the purely vegetative cells, a fact also established by other observers. These nuclei afterwards fuse and form a single nucleus, so that the mature spore is uni-nucleate. This fusion of the nuclei is regarded as a sexual act, equivalent to the conjugation of male and female pro-nuclei. The entire cell with its accumulated reserve material constitutes an oospore, which increases in size and surrounds itself with a thick membrane. Whether this is to be regarded as a sexual act or not depends upon the view we take as to the essence of the process. If it consists in the fusion of two nuclei, representing respectively the male and the female element, derived from more or less specialized cells and forming the single nucleus of a new generation, then the above does not conform to this view, where the blending nuclei are derived from *different* cells. The fusion of nuclei in the individual spore may serve the same purpose as reproduction by giving it increased vigour, but it is only where a fertile cell is stimulated to further development by the entrance of a nucleus from without that it is here regarded as true sexual reproduction. When the spore of *Ustilago*, for instance, germinates in water, the single nucleus passes into the germ-tube and divides, then a transverse septum is formed with a nucleus in each division, or the nuclei may divide further and become four, before the septa arise and form the typical four-celled promycelium. When the conidia are formed, each contains normally a single nucleus, which is derived from the division of the nucleus in the parent cell (Plate I., *q* and *s*).

In *Urocystis* and *Tilletia*, where the conidia are formed at the apex of the promycelium, the original nucleus becomes eight by successive bipartition, which pass in order into the apical conidia.

There is another phase of so-called sexuality which has long been observed in *Tilletia* and other genera, where the conidia unite in pairs. Two conidia become connected by a tube like the transverse bar in a capital H, and resemble very much the conjugating cells of *Spirogyra*, a fresh-water Alga. Such fusions were naturally suggestive of a sexual union, and De Bary maintained the view that they were analogous to a sexual process. In support of this view he observed, first, the almost invariable occurrence of pairing under the normal conditions of germination, as in water. Second, the union occurred, in the great majority of cases, between two and only two conidia. When an odd number of conidia were produced by the promycelium, they still united in pairs, and the odd one did not fuse with any of the others, although it would have been so easy and so natural to do so. This would seem to show that a change had taken place in the fused pairs which rendered a further union difficult or impossible. This view of De Bary was generally accepted as being the most probable explanation of the phenomenon, that the conjugation of the conidia was a sexual union. But Brefeld opposes this view, and considers the fusion a purely vegetative act, as occurs in the coalescence of vegetable cells. He regards the essence of a sexual union to lie in the fact that the conjugating cells are incapable of further growth by division, but become capable of further development as a result of their union. Applying this test to the conidia, he finds that they are individually capable of unlimited development when placed in nutrient solutions before pairing can begin, and that fusion does not occur under such conditions. He concludes that the fusions are purely vegetative, perhaps resulting from a process of starvation, for so long as adequate nourishment is supplied there is no appearance of conjugation.

Whatever view may be taken of the pairing of the conidia, whether of sexual value or not, it is a very characteristic feature in certain genera, and the nuclear phenomena underlying it ought to be taken into consideration. Dangeard, in investigating the conidia of *Tilletia*, found nuclei in the fusion tubes under such conditions that it suggested the view that they might serve as a means of equalizing the distribution of the nuclei. It might happen that, in the formation of conidia, some might receive two nuclei and some none at all, and the connecting tube would permit of the balance being restored. It would be interesting to observe in this connexion if the unpaired conidia always possessed a single nucleus only, for here we are merely dealing with a possible supposition still awaiting facts to support it.

CHAPTER IV.

Spore-formation in Australian Genera.

The mode of formation of the spores is often characteristic of different genera, and therefore it becomes necessary to see wherein the difference lies. The much-branched spore-forming hyphæ generally become greatly swollen, and their walls gelatinize. Then the spores arise within the old cells by the formation of a new membrane, and it is in the details of this process that variety occurs.

Ustilago.

The development of the spores has been closely followed by Fischer von Waldheim.[3] The fertile threads or spore-forming hyphæ become enlarged and excessively branched, and are densely crowded together. Then the gelatinization of the walls begins, and this proceeds to such an extent that the cavity is almost obliterated at first, only appearing as a narrow shining line in the centre of the hyphæ (Plate I., *e*). Next, a swelling of the surface of the hyphæ takes place at certain points, often close to one another, so that they appear nodose, and the cavity at the same time is enlarged. The hyphæ continue to increase in size and consequently become intertwined and tangled together, so that eventually they have actually coalesced. The irregularities of the hyphæ become more marked, and it is evident that the spores are beginning to be definitely formed as the swellings get more and more rounded. The crowded spore-forming hyphæ with their numerous branches, as they develop the spores, run together in a complex mass, so that their individuality is almost entirely lost (Plate I., *f*). They appear as a gelatinous mass studded with numerous shining points in the form of streaky or rounded bodies. The process of spore-formation, or the commencement of the differentiation of the protoplasmic contents to form a spore, is indicated by the entire mass of the hyphæ breaking up into distinct portions, which, however, retain their connexion with one another until the spores are completely formed and they are surrounded by a more or less dense gelatinous envelope. The spores become more or less polygonal from mutual pressure, but ultimately separate from each other and assume their typical spherical shape. The differentiated contents increase in size and contain fat granules, and a distinct contour is perceptible corresponding to the outer spore membrane. The outer edge of this contour darkens, and even while still surrounded by a thin gelatinous envelope, the irregularities of the epispore begin to appear. As the spores ripen the gelatinous membrane disappears and there is no trace of it at maturity, nor are any remains of the mycelial hyphæ attached to them, although it is often seen in Tilletia (Plate I., *k*).

Thus in Ustilago, the spore-forming hyphæ with their numerous branches are divided up by means of septa into short swollen cells, which become converted into spores. These are produced in an irregular manner, so that the entire mass of mycelium is ultimately transformed into a dark-coloured mass of spores (Plate I., *d*).

Melanopsichium.

In a cross-section of the rachis or axis of the inflorescence attacked by the smut the plant tissue is seen to be excavated by the fungus, leaving a central core more or less intact, and portions extending towards the epidermis. In these cavities the sori are produced and the spores are first formed at the centre of the sorus and gradually extend outward all round, so that the younger and

immature spores are towards the circumference, while the older and fully-formed are towards the centre. The sori generally surround the central core of plant tissue as in Cintractia, but the mode of formation of the spores is different. The sori, to begin with, are probably distended cells, and several of them run together so as to form a comparatively large cavity. In this way swelling and distortion occurs, somewhat similar to that of the Club-root of Cauliflower (Plate XXXIII.).

Cintractia.

A new genus was constituted by Cornu in 1883 on account of the development of the spores in a regular manner, radiating from a central columella of plant tissues and protected at first by a membrane composed of fungus cells. It was named in honour of a French botanist called Cintract. This genus is not universally adopted, as it is considered that the distinction between it and *Ustilago* is not sufficiently marked to justify its being retained, but the mode of development of the spores seems to be worthy of generic distinction. The mode of spore-formation has been described by Cornu[1] and Magnus[4]. The inner tissues of the host-plant form a central columella which is penetrated by the mycelium of the fungus, and this is aggregated into a compact, continuous, gelatinous mass surrounding the axis. The entire outer surface of this mass or stroma as it is called, may be fertile, producing spore-bearing filaments, or there may be sterile rays projecting at frequent intervals between the spore-bearing filaments. The spores are developed in the hyphæ as minute colourless portions of protoplasm surrounded by a gelatinous envelope. They are formed in succession, the oldest being always towards the outside and the youngest nearest the centre.

As they approach maturity, the gelatinous envelope is gradually absorbed, the gelatinous walls of the hyphæ disappear, the outer coat of the spore deepens in colour, and ultimately they are quite distinct.

In some cases the fertile layer or stroma is formed in the outer tissues of the host as described by Magnus[2] in *C. krugiana*, Magn. The mycelium growing luxuriantly in the parenchymatous and epidermal cells protrudes through the outer wall of the latter and forms on the outside a dense mass of interwoven fungus filaments in the interior of which the spores are developed.

The mass of hyphæ closely compacted and felted together on the outside constitutes the envelope or membrane together with the spore-forming hyphæ. The matrix from which the spores are formed adjoins the tissues of the plant, and the older ripe spores are on the outside, while the inner and younger spores are towards the base. This spore-formation occurs in a radial manner, and each row is separated from its neighbour by the mass of hyphæ between, which remains sterile. All the differentiated portions of the hyphæ of the matrix do not grow to mature spores. A large number of them only form a small cell cavity, and the gelatinous walls become swollen. They appear later to be absorbed, and probably supply material for the spores which grow to maturity.

The successive production of spores in spore-bearing filaments, arising from a so-called stroma, radiating outwardly and firmly agglutinated at maturity, is characteristic of Cintractia, but the sterile rays are not always present.

Sorosporium.

In this genus the spores are in clusters and not separate and distinct as in Ustilago. Fischer von Waldheim[3] has investigated their formation in *S. saponariae*, Rud., and it is as follows :—The extremely abundant mycelium in the blossom and ovary rapidly changes into spore-forming hyphæ, from 4 to 7 μ in diameter, and like those of Ustilago are gelatinous and full of shining

protoplasm. At the same time, the hyphæ give rise at various points to inwardly curved branches, and several of these branched spore-forming hyphæ lay themselves together and twist themselves into a small ball, not unlike what happens in the formation of a lichen-thallus. These convoluted and contorted hyphæ, being gelatinous, soon become so intertwined and entangled that they lose their individuality, and on the exterior of this gelatinous ball other hyphæ are seen encircling it. These hyphæ are also gelatinous and soon become indistinct, although sometimes there are traces of a concentric arrangement. Spore-formation is confined to the central gelatinous ball in the middle of which it commences as circumscribed clear spots, which soon assume a distinct outline, become brownish in colour, and are differentiated into spore-like bodies varying in number from four to sixteen, or even more. These bodies again subdivide, so that when the spores arrive at maturity there are sixty to a hundred, or even more of them, in a spore ball. In the young state these developing spores are polygonal from mutual pressure, and they are to be found in spore-balls not more than 50 μ in diameter. In the subsequent development of the spores, the ball increases in size and the gelatinous zone swells also, but when the spores assume their characteristic deep brown colour, this gelatinous zone begins to be absorbed, having been utilized in the development of the spores. In spore-balls of 70 μ in diameter, the gelatinous zone is only from 4 to 6 μ thick, and there is no trace of it in the fully matured spore-balls, except occasionally as in *S. solidum*, where the remnants were at first regarded as sterile cells like those in Urocystis.

In a section of the affected portion of the host-plant concentric layers of spore-balls to the number of six to eight occur, the peripheral layer being the oldest, having been pushed outwards by the continued formation of the young spore-balls in the centre.

Thecaphora and Tolyposporium.

The development of the spores has not been completely traced in these genera. The spore-bearing hyphæ are intertwined and interlaced into a dense mass, and the early stages of the spore-balls are difficult to determine.

Tilletia.

The formation of spores in this genus has been investigated by several, but it is to Fischer von Waldheim that we owe the most complete account of the process which is as follows :—When spores are about to be formed, the spore-bearing hyphæ give off pear-shaped buds in succession from their sides. (Plate I., *g*). These outgrowths increase in length, and at the same time the swollen end of each increases in diameter and becomes rounded, so that it is ultimately attached to the hyphæ by a thin stalk (Plate I., *h*). The contents derived from the hyphæ are granular and vacuolated and particularly rich in oil, and the membrane becomes somewhat gelatinized. Just before reaching maturity the gelatinized membrane is absorbed and the young spore acquires a double contour, the epispore gradually becoming darker and uneven (Plate I., *i*, *j*). In some cases the gelatinous membrane of the hyphæ invests the spores up till the time of ripening, and then disappears without leaving any trace. The stalks or connecting branches soon wither, and to many ripe spores their remains continue attached (Plate I., *k*).

While in Ustilago the spore-bearing hyphæ directly break up and form the spores, in Tilletia the spores are formed singly at the ends of branches.

Entyloma.

De Bary[3] has investigated and described the development of the spores, and it is found to be very similar to that of Tilletia. The fertile mycelium

is much branched, and the spore-forming hyphæ become swollen at certain places along their length as well as at their ends. The contents of the cells acquire the characters of spores, so that they are marked off or intercalated between certain portions of the hyphæ. In Tilletia the spores are only formed at the ends of the branches. In this intercalary formation a series of spores may be seen arranged in regular succession with the intervening remains of the hyphæ. When mature, they do not break up into dusty masses, but remain embedded in the tissues of the host-plant. Each mature spore possesses two coats, and the outer coat is sometimes gelatinous.

Urocystis.

The development of the spores has been studied principally by De Bary, Wolff, and Winter. The spores are produced in compact clusters with a special envelope of sterile cells, and the mode of formation of both these structures has been generally followed. The spore-forming hyphæ branch at their free ends, and the first beginning of a cluster is indicated by the branches becoming swollen and curved, and winding themselves round each other generally in a spiral manner, so as to form a glomerulus or ball.

Their walls become so gelatinized that they run into each other and blend so that they are quite indistinguishable from one another. The spores are formed entirely from these gelatinized central balls and consist of a group of cells firmly bound together. Each cluster of spores is surrounded at an early stage by slender curved branches from the hyphæ, and these outer branches closely invest the spores and form the envelope. These investing hyphæ, as De Bary has shown, divide into short cells by means of transverse septa, and, while most of them disappear as the spores ripen, a number varying with the individual species persist and form the envelope of the mature cluster of spores. The number of spores in a cluster vary and sometimes there is only one surrounded by its sterile envelope.

Doassansia.

Cornu, who founded the genus, Fisch, and Setchell have studied the development of the spores. When a sorus is about to be formed, the hyphæ give off numerous interlacing short branches which are soon formed into tangled knots. It is from these knots that the spores are formed. The cells of the hyphæ in the interior of the knots become swollen and form a mass of large, thin-walled, polygonal cells, which become the spores, the process being accompanied by a gelatinization of the walls. The external portion is at first composed of compact layers of almost unaltered hyphæ, but shortly before the ripening of the spores the "cortex" of sterile cells is indicated. These appear just beneath the reduced layer of investing hyphæ and are probably formed from a layer of cells similar to and adjoining those from which the spores are formed. The sterile cells gradually become oblong or wedge-shaped, lose their granular contents, and are filled with air, taking on the brown colour of the wall characteristic of maturity.

CHAPTER V.

Germination of Spores.

The spores may either germinate in water or in a solution to which nutritive material has been added. The germination of spores in nutrient solutions has been studied in great detail by Brefeld, and has been shown to differ somewhat from that obtained when only water is supplied. The first to employ nutrient solutions in studying the germination of smut spores seems to have been Hallier[1] in 1868, who used a variety of substances, such as starch paste, white of egg, milk, a solution of sugar, &c. In every case where germination has been carried out by myself it was first tried in water, and then usually in some definite nutritive medium for comparison.

The process of germination, wherever known, is given in connexion with the various species, since it furnishes important systematic characters; but a general account is given here of the usual course of development. When the spore begins to germinate under the influence of moisture, it puts forth a longer or shorter germinal tube, known as a promycelium (Plate I., *m*, *n*, *p*, *r*). Then small hyaline spore-like bodies are, as a rule, produced, called promycelial spores or conidia (Plate I., *q*, *s*). In those cases where infection of the flower takes place, as in Loose Smut of Wheat, a much-branched mycelium is usually formed without any conidia, and here we have an instance of the germinal tube developing directly into a mycelium.

When conidia are formed, they may directly produce a germ-tube which infects the proper host-plant and develops a mycelium, which again reproduces the spores. Or they may bud even while still attached to the germinal tube, and give rise to secondary or tertiary conidia, which may in turn germinate and penetrate the tissues of the host-plant. It happens not infrequently that the conidia unite in pairs, even in some cases before they have become detached from the promycelium. A short transverse tube connects adjacent pairs, and the protoplasm of the two is placed in direct communication. This pairing is regarded by De Bary as a sexual act—a process of conjugation; but Brefeld considers it as analogous to the blending which takes place between different branches of a mycelium. However that may be, after this union has taken place, a slender germ-tube is produced which receives all the protoplasm from the paired cells, and can infect the proper host-plant where it develops a mycelium, which in turn produces a crop of smut spores. This may happen either with solitary or paired conidia. While the spore follows the general course of development sketched above when germination takes place in water, it is somewhat different when a nutrient solution is supplied. Hallier[1] observed that in rich nitrogenous substances, such as white of egg, the germinal tubes were thick and distorted, but he also considered that they changed into various moulds from his cultures not being pure. It was Brefeld, however, who was the first to successfully apply nutrient solutions to the prolonged and pure culture of smut spores. He mostly used a sterilized decoction of fresh horsedung, and found that when such a solution is employed the germination is not only more rapid and much more luxuriant, but that it can be kept up indefinitely as long as nutriment is supplied and the reproductive bodies themselves are sometimes different. He soon found that water alone was

not the most suitable medium for obtaining the best results. In many cases the conidia were formed, but they were often so passive that they did not germinate, and without some additional means of quickening their germination and development it was difficult to account for the wide distribution of the smuts. I have found a sterilized infusion of hay a good culture medium, and have also used a variety of substances, such as malt extract, soil extract, somatose, Cohn's modified solution, &c.

In some cases it is very difficult to get a spore to germinate even when the various nutrient media are tried in addition to water. It may be that it is not the proper season of the year, and some spores may require a rest before starting germination. I may take *Ustilago calandriniæ*, Clint., as an illustration of this class of spore. The spore is of the Tilletia-type, with regular reticulations of the epispore, and it was desirable to germinate it in order to settle the genus. The only material in my possession at first was fully ten years old, and it failed to germinate; but that might be owing to its age. Fortunately I came across fresh material in October, 1908, and it was also supplied to me in November, as well as in January, 1909. The fresh spores were placed in both tap and distilled water, as well as in a decoction of the plant itself, also in ammonium nitrate, lactic acid, tannic acid, an infusion of sugar-beet, sugar solution, and Cohn's modified solution. At the end of six days only a very few germinated in distilled water and formed conidia, as in Ustilago. But in the other solutions, although some of them were kept till the fourteenth day, there were no signs of vitality.

In proper culture media the spore germinates as usual, and produces a germinal tube, but instead of remaining short and forming conidia, it often continues to develop and gives rise to *sprouting conidia*, which multiply by budding after the manner of yeast. Or the germinal tube may grow luxuriantly and produce a much-branched mycelium, from which in the fluid itself or in the air conidia are formed. These conidia sprout at the end again into one or several conidia, and we may distinguish them as water or air conidia, according to the medium in which they are produced.

There is thus a great variety of reproductive bodies, although there is only one kind of spore, and it is quite likely that the conidia, sprouting conidia, and aerial conidia of the smuts are just as efficient means of distribution as the different kinds of spores among the Rusts.

A word of caution is necessary, however, as to the interpretation of results obtained from "pure cultures," as they do not necessarily represent what actually takes place under natural conditions. The researches of Klebs,[1] Kaufmann,[1] and others have shown that the formation of reproductive organs of a particular kind or their suppression is largely determined by food and environment. Klebs was able to control at will the reproductive processes in certain fungi, according to the composition and concentration of the nutrient medium, as well as by the temperature, presence or absence of light, &c. There is no reason to doubt that the same principle applies to smuts, and that it will tend to explain the discrepancies in the results obtained by different observers in the germination of the spores under different conditions and in different media.

As has already been shown, the germination of the spore is not always easy of accomplishment, for we do not always know the precautions to be taken. Some spores are capable of germination immediately after being gathered, others require a period of rest. Some germinate in the water or

other liquid medium, others on the surface of it, and still others require only damp air, for if they come in contact with water they are abnormally developed. The time required for germination is also very variable, as it may occur within a few hours or take several days, as in the case of *Tilletia tritici*. No doubt this is dependent on various factors, such as the age of the spore and the conditions of the weather, which is most favorable when it is warm, damp, and cloudy.

Duration of Germinating Power.

In quite a number of cases the spores are capable of germination as soon as they are mature, and where cereal crops are concerned, this immediate germination would evidently tend to the extinction of the fungus, since there would be no suitable host-plant to infect at that season, and so the conidia formed would probably perish. But it is now known that under such circumstances special conidia are formed, which have the property of living on dead or decaying vegetable matter, and thus tiding the fungus over the period when living plants are not available. In the case of Loose Smut of Oats, for instance, Brefeld brought about infection by means of the sprouting conidia derived from the budding conidia grown in a nutritive solution. In other cases the spores are only capable of germination after a period of rest, and so are ready to infect the host-plant at the next period of vegetation. This period of rest may extend over a number of years, if the conditions are not favorable for germination. Thus the bunt spores have been known to retain their vitality for eight years and a half when kept perfectly dry, and the spores of *Tolyposporium bursum* on kangaroo grass have germinated after four years, the spores having been collected in November, 1902, and germinated towards the end of 1906.

Types of Germination.

It was formerly taken for granted that smut fungi could only live and grow upon the host-plants with which they were found associated in nature, and experiments and observations were accordingly confined to these hosts. It was known that the spores could germinate in water just as they would on the moist surface of the plant, but beyond that there was no independent existence supposed to be possible. When it was discovered, however, that these smut spores could live and grow outside of the host-plant, then it was realized that their developmental history could be followed apart from the living organism. It is to Brefeld we owe this new point of view, which has been so fruitful in results, and the use of artificial nutrient solutions, instead of mere water, was the starting-point.

By studying the germination of spores in this way we have learned that there are various types of germination, and concrete examples, occurring in Australia, will be given of each type.

1. In *Ustilago avenæ* the germinating spore produces a germinal tube bearing conidia, and these conidia multiply rapidly *in the liquid* by sprouting in a yeast-like manner at both ends. (Fig. 1.)* Each of these daughter conidia is capable either of repeating the sprouting in a nutritive solution or of directly infecting the young seedling.

* Text figures are simply referred to as Figures, while those belonging to the Plates are always preceded by the number of Plate.

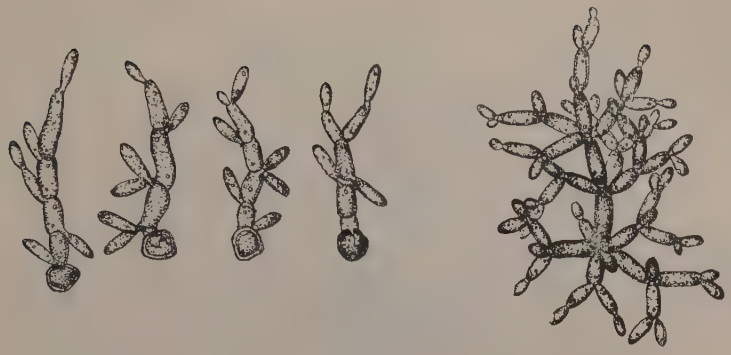


FIG. 1.

a. *b.*

Fig. 1.—*Ustilago avenæ* or Oat Smut.—*a*. Spore germinating and giving off conidia from germinal tube or promycelium × 450. *b*. Colony of sprouting conidia, developed from one of the conidia in *a* × 350. (After Brefeld.)

2. In *Ustilago bromivora* the conidia produced by the germinal tube are not sprouting conidia, but they form new germinal tubes or promycelia, which in turn produce similar conidia. (Fig. 2.) As a rule the promycelium is only formed once direct from the spore, but here it is repeated, and is not confined to the germinating spore.

FIG. 2.

Fig. 2. *Ustilago bromivora* or Brome Smut.—A single spore producing a two-celled promycelium, which forms conidia, and these conidia in turn again develop a promycelium, and so on until quite a number is formed, as in Figure × 400. (After Brefeld.)

3. In *Ustilago olivacea* the germinal tube is in abeyance, and conidia are formed direct from the spore. These conidia multiply indefinitely in a nutritive solution by sprouting in a yeast-like manner. (Fig. 3.)

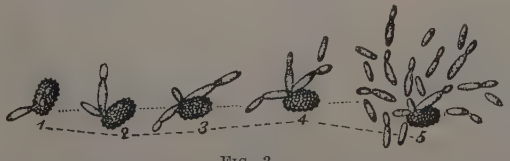


FIG. 3.

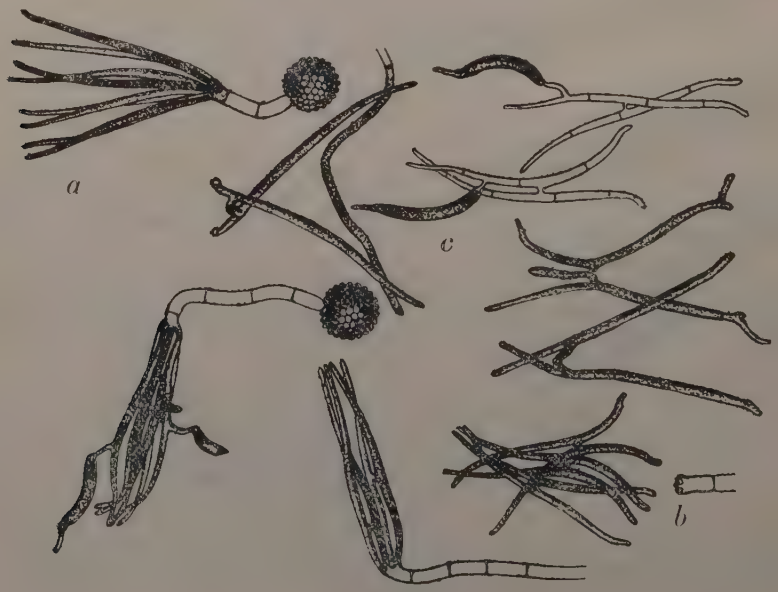
Fig. 3. *Ustilago olivacea* or Carex Smut.—Spores producing conidia direct without the intervention of a germinal tube × 400. (After Brefeld.)

4. In *Ustilago nuda* the germinal tube does not produce conidia at all, but grows out into a large and copiously branched sterile mycelium. (Fig 4.)

FIG. 4.

Fig. 4. *Ustilago nuda* or Naked Barley Smut.—Spore germinating and producing a much-branched mycelium × 350. (After Brefeld.)

5. In *Tilletia tritici* the germinal tube produces a tuft of conidia at its apex, and each of these conidia or the conidia united in pairs produce a single secondary conidium capable of infecting the wheat plant. Or the conidia may produce a large and richly-branched mycelium *in the air*, just like a tuft of mould from which aerial conidia again arise, and this process is repeated as long as the nutrient solution lasts. (Fig. 5.) The important fact is here made evident that the smut fungi can reproduce themselves saprophytically, and that these reproductive bodies are found to be capable of infecting the proper host-plant and of producing the disease.



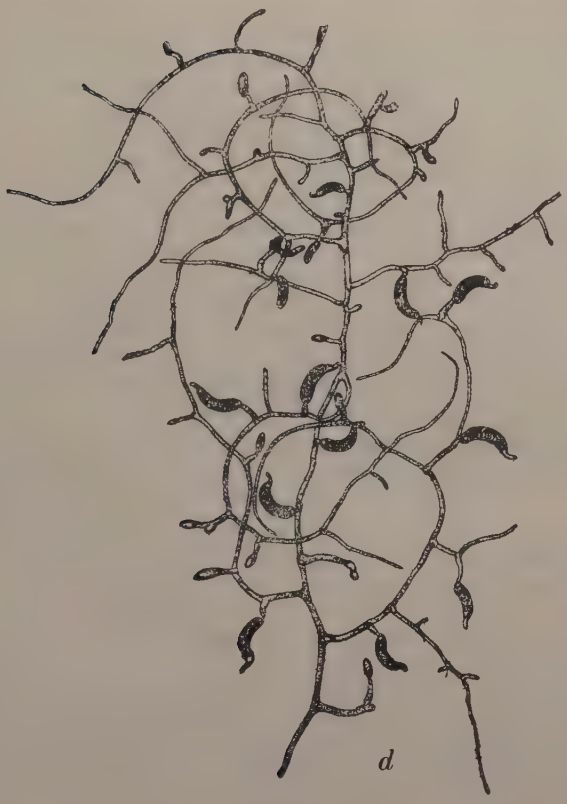


Fig. 5.

Fig. 5. *Tilletia tritici* or Bunt of Wheat.—*a*. Germinating spores with septate promycelium bearing elongated conidia at apex × 300. *b*. Apex of promycelium from which the six conidia fused in pairs have become detached × 250. *c*. Conidia detached and fused in pairs, and some bearing sickle-shaped conidia × 400. *d*. Mycelium like a tuft of mould produced from conidium and bearing sickle-shaped conidia in all stages of development × 350. (After Brefeld.)

Effect of Light and Darkness on Germination.

I tested the germination of some of the more rapidly germinating spores, such as those of *Ustilago readeri* in light and in darkness. Spores were taken from plants of *Danthonia penicillata*, collected on 6th December, 1908, and placed on slides in ordinary tap water on 6th January, 1909. Some were kept under a bell-jar exposed to the light and others in a seed germinator in which the light was excluded, but the air admitted. Both were kept in the same room, the only difference being the presence or absence of light. The experiment was repeated several times and invariably light was proved to favour germination.

In one experiment, the slides were examined after five hours, and while a few of the spores exposed to the light had germinated, none had done so in the dark. After twenty-four hours, they were again examined, and the great majority of the spores had germinated in the light, while only a few had germinated in the dark. In the light, promycelia were formed which sometimes

grew out into slender elongated filaments, but no conidia were formed. In the dark a few of the promycelia produced one or two conidia. In another experiment, there was no germination after two hours, but in four hours occasional spores in the light had produced promycelia about twice or thrice as long as the spore, while in the dark only a very few had germinated, and the promycelia were much shorter, only about the length of the spore. At the end of twenty-four hours the slides were again examined. In the dark only a comparatively few of the spores had germinated. The promycelia varied in length from 30 to 52 μ, either without septa or 1-3 septate, and bearing sometimes one or two lateral and a terminal conidium. Only in rare cases was a conidium produced at the end of another while still attached. In the light there was luxuriant germination, and the great proportion of the spores had germinated. The characteristic feature was that the promycelia grew out into long, slender, often wavy filaments, which readily became detached, reaching a length of 200 –300μ. Only rarely were conidia formed, and sometimes two promycelia proceeded from the same spore.

I have only tested the effect of light and darkness on the one species of spore, but Fischer von Waldheim[3] also found that the germination of smut spores was retarded by withholding the light—that light had a stimulating effect on germination. In *Ustilago carbo* (= *Ustilago avenæ*) it delayed the germination for several hours, and also caused the promycelium to be frequently bent in a knee shape.

Effect of Exposure to Sunshine on Germination.

It is a common belief among farmers that long exposure to the sun's rays in summer kills the bunt spores, and they account for the general absence of bunt in self-sown wheat by the spores on the exposed grain being destroyed in this way. Laurent[1] was induced to investigate the subject by observing that in some districts a burning sun at the time of sowing the wheat diminished the chances of infection. He took bunt spores and exposed them to the full sunlight in a glass vessel, and at the same time he exposed other spores to the same light passed through a layer of a solution of sulphate of quinine three centimeters thick. The temperature of the surrounding air did not rise above 40° C. After eight hours it was found that the spores fully exposed to the sunlight did not germinate at all, even in a nutrient solution of unfermented beer, while the spores shaded entirely from the sun germinated freely. The spores which were shaded from the chemical rays of the sun by the solution of sulphate of quinine did not lose their germinating power, even after sixteen hours of exposure to a very hot sun, so that it may be assumed that while the exterior spores of a bunt-ball are killed under these conditions, the interior spores are still capable of germination.

Farrer[3] also carried out experiments to test the effect of dry heat on bunt spores, and since it was believed that soaking the seed wheat in water for a quarter of an hour at 57° C. had the effect of killing the spores, he tried this heat in the dry state, as well as higher temperatures for the same time. The result was that the higher the temperature the smaller was the proportion of seeds which produced plants, and the greater the proportion of plants which were bunty. At 54° C. of dry heat about 2·6 per cent. of the infected grains lost their germinating power and 3 per cent. were bunty, while at 104° C. three out of 136 seeds grew, but none formed ears. The direct heat of the sun may have a different effect on spores than dry heat, yet Farrer[5] says :—" My experiment with dry bunt shows conclusively, I think, that it is not the heat of the sun which kills the spores of bunt which are left on the ground; it is, I think, moisture—the moisture from rains and dews, the moisture which comes

from below to the surface of the soil, and possibly also the invisible hygroscopic moisture which the soil and vegetable matters absorb at night, especially on nights when the fall of temperature is considerable—which causes the great majority of the spores which are left in the ground to germinate. When this happens, the absence of hosts (freshly germinated wheat-plants) to attach themselves to and dry weather soon causes the young bunt-seedlings to perish." It is probable that both methods occur in nature, and that while the exposed spores are acted on by the sun's rays, those protected by the soil or otherwise are induced to germinate by the moisture and perish in the absence of a host-plant.

Effect of Temperature on Germination.

Eriksson found that the spores of some rusts germinated more freely after being exposed to a temperature of 0° C., or even less, although an extremely low temperature retarded germination. Schindler[1] experimented with some smuts and found that with a dry heat the spores of *Tilletia tritici* could stand 65° C. without losing their power of germination, but with a moist heat of 45–50° C. they were rendered sterile. Cold, on the other hand, produced but little effect, even after prolonged exposure to −20° C.

* * * * * * *

In preparing slides of germinating spores for photographic purposes, the water is first allowed to evaporate under cover, then absolute alcohol is added as a fixing agent. This is gently moved to and fro for a few minutes, and after drying, the stain is directly applied. The most generally useful stain is Bismarck Brown, which gives a beautiful golden-brown tint to the promycelia and conidia. Although it stains quickly the specimen may be left in it for at least twenty minutes without injury. The excess of stain is next drained off or washed off, and, if too deeply stained, it can be rendered lighter by the application of dilute alcohol. The object is then mounted in glycerine and water (half and half) in the usual way.

CHAPTER VI.

Infection.

After the germination of the smut spores had been observed for a large number of species, the mode of entrance into the host-plant and the further development there until spores were again produced, was carefully studied by a number of botanists. Among the most prominent investigators were De Bary, Kuehn, Fischer von Waldheim, Wolff, and Brefeld. They determined the mode of infection in certain species, but a number still remain in which the exact method of germination and infection has yet to be discovered.

It was generally found that infection occurred in the seedling stage of the host-plant by means of the spores, which germinated and produced their conidia. The young seedlings may be infected either by the smut-spores attached to and sown with the seed, or they may be in the soil. While the spores of some species of smuts remain in the soil in an inactive condition, there are others, such as the flag smut, in which the infection is principally from the soil. Brefeld[1] showed in his experiments with loose smut of oats that seed sown in an infected mixture of field soil and fresh horse-dung yielded between 40–50 per cent. of smut; but his[7] recent similar experiments with the loose smut of wheat and barley for three years in succession only yielded negative results. The reason for these negative results lies in the fact that infection does not occur in the seedling stage, but through the flower, as we shall afterwards see. It is principally owing to the patient and long continued investigations of Brefeld that our previous views regarding the modes of infection have had to be considerably modified, and, in accordance with this, the methods of treatment have been placed on a surer foundation.

Infection and Contagion.

When Meyen contended that the smut is not a contagious disease but is inherited, he simply meant that it was not due to any external parasite, but was inherent in the plant itself. Infection and contagion were in his time regarded as synonymous, but now the latter term is generally applied to those infectious diseases in which direct contact is necessary to produce them. There is no necessity for the plants to be actually in contact in order to contract the disease caused by the smut fungi, but the spores or germs are conveyed to the plants, and so we speak of infection. Infection does not consist in the mere penetration of the germ-tube of the spore or conidium through the epidermis into the tissues of the host-plant, but the germ tube must grow and develop at the expense of the living cells until it reaches the apex of growth, and there become associated with the growth of the host, so that finally fresh spores are formed. It is well known that the germ-tube of the smut fungi may penetrate inside a plant, and there die off without producing any injurious effect, and for convenience we might use the term inoculation to signify merely that the spores or germs had been applied to an otherwise healthy plant, while the normal infection would consist in the entrance and growth of the germ-tube within the tissues of the plant and the final production of spores. The period which elapses between the infection and the production of spores through the multiplication of the fungus inside the plant might also be called the "incubation period." Thus, in the case of stinking smut, the incubation period extends from the infection of the seedling to the production of spores in the ovary, and in the case of the American corn smut, where infection is strictly confined to the young parts

of the plant directly attacked by the fungus, the period of incubation is within fourteen days. It has also to be noted that numerous infections may occur in the same plant at the same time. Brefeld removed the epidermis from young seedlings that had been infected, and found it pierced by distinct holes, through which the germ-tubes had entered. In favorable preparations he observed the surface riddled as if by drill holes and permeated by numerous in-grown germ-tubes. This would explain such cases as I have met with where ears from the same plant produced spores of both *Tilletia tritici* and *T. levis*, for if the grain was dusted with both kinds of spores they might both infect the same plant. Even the case mentioned by Sorauer[1], where both species were found in the same ear, could be explained in the same way. It is not unusual to find cases with stinking smut and loose smut on different ears from the same wheat plant, but this is not difficult to account for. The loose smut fungus was already in the grain of the wheat plant, since infection takes place through the flower, and afterwards infection occurred in the seedling stage by means of the spores of stinking smut.

Modes of Infection.

There are at least four typical modes of infection at present known, and by giving a detailed account of each subsequently it will serve to show the nature of the process and the means most likely to be successful in combating the particular disease.

1. The most common mode is that the young seedlings are infected, the resulting mycelium grows throughout the entire plant and the smut spores are produced usually in the flowers or inflorescence, as in oat smut (*Ustilago avenae*).

2. A second type is represented in the case where any young and growing portion of the host-plant is capable of infection, and the mycelium is localized where the infection occurs, as in the American corn smut not known in Australia (*Ustilago maydis*).

3. Infection may take place through the stigma of the flower, the spore acting after the manner of a pollen-grain, or by piercing the young ovary wall, the mycelium developing in the ovary, lying dormant in the ripe grain and growing throughout the entire plant next season, until it reaches the flowering stage, when the smut spores are again formed, as in loose smut of wheat (*Ustilago tritici*) and naked smut of barley (*Ustilago nuda*).

While in the cereals it is generally considered that the wind is the agent for carrying the spores to the stigma or ovary after fertilization has occurred, it is highly probable that thrips are also concerned in it, for in our northern areas particularly, these insects are in some seasons so common as to affect the development of the ears of wheat.

4. Infection may take place as shown by Hecke,[4] through the young shoots which arise near the surface of the soil in the process known as "tillering."

It is worthy of note that these different modes of infection are associated with a different behaviour of the spores on germination. In the first and fourth type sprouting conidia are formed which are capable of living saprophytically in the soil and infecting the plant from that source. In the second aerial conidia are chiefly formed, and infection is mainly brought about by the wind; and in the third no conidia are formed at all, so that the spores are carried to the stigma and germinate there after the manner of pollen-grains, or they may fall upon the surface of the very young ovary.

1. Seedling Infection.

This was at first considered to be the only mode of infection, as it was the only one known, and even now it is recognised as by far the most common. The spores are generally attached to and sown with the seed, and if both germinate at the same time infection usually occurs. The spore on the moist surface of the grain germinates and produces its germinal tube bearing conidia. The conidium stimulated by the moisture puts forth a delicate germ-tube which penetrates the young tissues of the seedling if it reaches it at the right time. The particular spot for infection is at the junction of the rootlet just emerged with the young shoot still within the seed, and this is sufficiently delicate to allow the germ-tube not only to reach the growing point of the primary shoot, but to branch out into any secondary shoots that may be formed.

But the question has also been raised as to soil infection, whether the spores in the soil and not on the seed will infect the host-plant. As already stated, Brefeld has shown that this may occur with loose smut of oats (*Ustilago avenae*), and I have elsewhere proved by experiment that soil infection occurs in flag smut of wheat (*Urocystis tritici*). With regard to stinking smut of wheat, Bolley showed that when the spores winter in the soil they do not infect the second crop, as they have already germinated by that time. If smut-balls are in the soil, however, they may cause infection. Seed was sown close to smut-balls in the ground, and it was found that when the seed was untreated the spores of the smut-balls reached the seed, and infected it, while seed under similar conditions and treated with bluestone was unaffected.

It would appear also that the greater the proportion of spores on the seed sown the more severe the infection. Thus in inoculating the grain with bunt spores, when one ball of smut was applied to a hundred wheat grains, the percentage of smutted plants in two cases was 56 and 58 respectively, while when the spores were applied at the rate of one bunt ball to five grains, the proportion was 79 and 81 per cent. respectively.

2. Local Infection.

This is seen to perfection in the American corn smut (*Ustilago maydis*), where any young and growing portion of the host-plant is capable of infection and the action of the fungus is strictly localized to these particular spots. Brefeld[3] carried out an extensive series of experiments in which he proved that only those parts of the young plant become smutty which have been directly infected, all the rest remaining perfectly normal, so that the action of the germ is strictly localized. He began by inoculating young seedlings with sprouting conidia produced upon a nutrient solution, and the few plants which developed the smut swellings died completely. In those cases, however, where the axis remained sound he expected to find smut developed in the ears as in the case of grain smuts, but not a single plant was smutty. This was contrary to the idea then prevalent that infection could only take place through the young seedling and he came to the conclusion that the germ-tube might penetrate into other parts which were in a young condition similar to the seedling. Accordingly he infected the heart of the plant still growing, and the result was that "the entire leaves were covered with a complete crust of pustule, which, in part, made them almost unrecognisable." He next infected the fertile inflorescences in the bud condition, and none escaped. Where the lower flower buds were infected, and not the upper, the latter always remained sound, and even where the exposed ovaries at the tip received the germs, they were swollen and smutted, while the ovaries lower down on the same spike produced normal grains. The adventitious roots which

appear on the lower nodes of the axis were also infected as soon as their tips were exposed, and they, too, soon showed swellings which developed into smut pustules. Thus, wherever the tissues were young and tender, the germinating conidia were able to penetrate and produce infection which, however, was strictly confined to the parts directly attacked.

3. Flower Infection.

Infection through the flower has only been recently experimentally proved, and on account of its practical importance, will require to be fully considered. For this mode of infection, those smuts are best adapted which have powdery spores, and are, consequently, easily blown about by the wind. What are known as Loose or Flying Smuts, fulfil these conditions perfectly, as the very name indicates that they are readily scattered, and those of wheat and barley are characteristic examples.

As far back as 1896, Mr. Frank Maddox, then Agricultural Experimentalist to the Council of Agriculture of Tasmania, had practically demonstrated infection by the flower, and his account of it in the *Agricultural Gazette* is well worthy of being reproduced here. He writes :—" I will now give the conclusions I have arrived at with smut (of wheat) from the results of my experiments. I have never been able to cause infection and reproduce the disease with spores on the grain or in the ground, which I can so easily do with bunt spores to reproduce bunt. The only way I have been able to infect grain and reproduce smut (which seldom ever fails) is by putting the spores on the ovary of the plant at flowering time, about the same time as the pollen-grains are being shed. The grain will mature without the slightest signs of being diseased. I have hit the time so well now that I may say I never have a failure. I think this accounts for when I did fail, viz., the ovary was not forward enough for the spore to get its seed-bed, or possibly, sometimes the spores were not matured enough. The comparison of bunt and smut spores finding their seed-bed are the very opposite. It is really wonderful to me how the smut spores do, as the ovary is well protected by the glumes or chaff, and there is only a short period that infection seems to be able to take place." There is no doubt that here we have a practical demonstration of the fact that infection by the loose smut of wheat occurs during the flowering period, and that this is the first record of it.

Next year, in 1897, Nakagawa[1] infected the flowers of wheat with the matured spores of loose smut. The infected seeds were sown, and next year the plants were found to be smutted. Soon afterwards, similar results in flower infection with the spores of *Ustilago tritici* and *U. nuda* were obtained by Hori[1], and he concluded " that the spores of those smuts which mature at the flowering time of the host, and may be scattered easily by the wind, will be retained in the inner side of the seed and give rise to the smut disease during the next flowering time of the host-plant."

In 1903, Brefeld[6] had also proved flower-infection in the wheat, and Hecke[2], in 1904, the same in the barley. In 1905, Brefeld published a series of carefully conducted experiments. Spore material of the loose smut of wheat carefully selected and preserved through the winter, was dusted on to the stigma of the wheat-flower, just as in the operation of crossing, and microscopic examination showed that the spores germinated, and that the germ-tubes passed down the style into the ovary, where a fine network of mycelial filaments were formed. But the plants thus treated exhibited no signs of disease and produced strong healthy grains in the ear. When the grains, however, were sown next season, with all necessary precautions against outside infection, the resulting plants were so badly affected that the entire inflorescence was destroyed. As the same result was always repeated the conclusion

became irresistible, that this smut exclusively infects the flower, and that it is not developed in the same year but remains latent in the mature grain. When this grain is sown next season, the mycelium passes into the young plant and then, on reaching the inflorescence, proceeds to the formation of smut spores. It is very evident, therefore, that it was the mycelium in the seed which caused the disease, for the grains were sterilized and disinfected before sowing, so that every chance of infection from spores adhering to the grain was excluded. Further, to protect them against contamination in the soil, the grains were sown in germinating chambers on a layer of sterilized sand, and when the developing grains had reached the immune stage, the plants were carefully laid out and grown in the open.

The methods adopted by Brefeld in carrying out experiments to prove that infection took place through the flower, are of sufficient interest to justify mention of them, and they were such as approached most nearly the natural infection. The most favorable time was when the flowers were most fully opened and the spores were powdery and easily scattered, conditions met with in dry sunny weather. As the result of various preliminary trials, Brefeld found that a hollow India-rubber ball was the best for applying the spores, an apparatus similar to that used for applying "Mortein," only the ball was larger. The smutted inflorescence was introduced into the ball and a tube inserted in the opening, so that the smut spores could be forcibly blown out in the form of a fine spray. The ears to be infected were placed in a glass cylinder, closed below by cotton wool, and the spores were blown in from above. After a short interval to allow the spores to settle, the ears were removed from the cylinder and thus infection of the flowers alone was made the subject of the experiment.

Of course only a limited number of flowers open at the same time to allow access to the spores, for it is well-known that they do not open all at once, but generally those in the middle of the ear are most advanced, while those at the top and bottom are later. Hence with only one infection a certain proportion are always missed, and there is no advantage in infecting the same ear at different times, since the necessary handling hinders the normal development. When infection takes place in the field, the chances are proportionately increased, for the spores are being constantly scattered upon adjoining healthy plants with the slightest breath of wind, and it is only interfered with by rain or damp weather. Warm and dry weather is also unfavorable for the germination of the spores, while it hastens the ripening of the grain.

A second and more delicate method consisted in the artificial infection of each flower, just as in cross-fertilization, using a fine camel's hair brush to dust the spores on the stigma of the flower.

This is more reliable than the "cylinder-infection," since all flowers not infected may be removed, but it must not be assumed that each flower left is actually infected, for all the flowers of an ear are not capable of infection at the same time. By either of these methods, flower infection experiments were carried out on wheat and barley, and while the grains produced seemed quite healthy and normal, yet on being sown the following year under strict sterilization conditions, smutted ears appeared at harvest time in greater or less proportion. Although Brefeld succeeded in inoculating the wheat-flower, for instance, and observed a few days afterwards that the spores had germinated in the stigmatic secretion and had sent hyphae through the stigmatic tissues to the ovary, yet it must not be assumed that this is the only way in which flower infection takes place in nature. It is well-known that the flower of wheat is self-fertilized before opening, so that the smut spores will, in all probability, fall upon the young ovary wall when exposed and thereby gain an entrance.

Hecke[3], in 1905, also demonstrated that the mycelium of the fungus was in the embryo of the barley, even while still enclosed in the seed, after the infection of the flower with the spores of naked smut. This anatomical proof places the fact of flower-infection on a sound basis (Fig. 6). Flower-infection

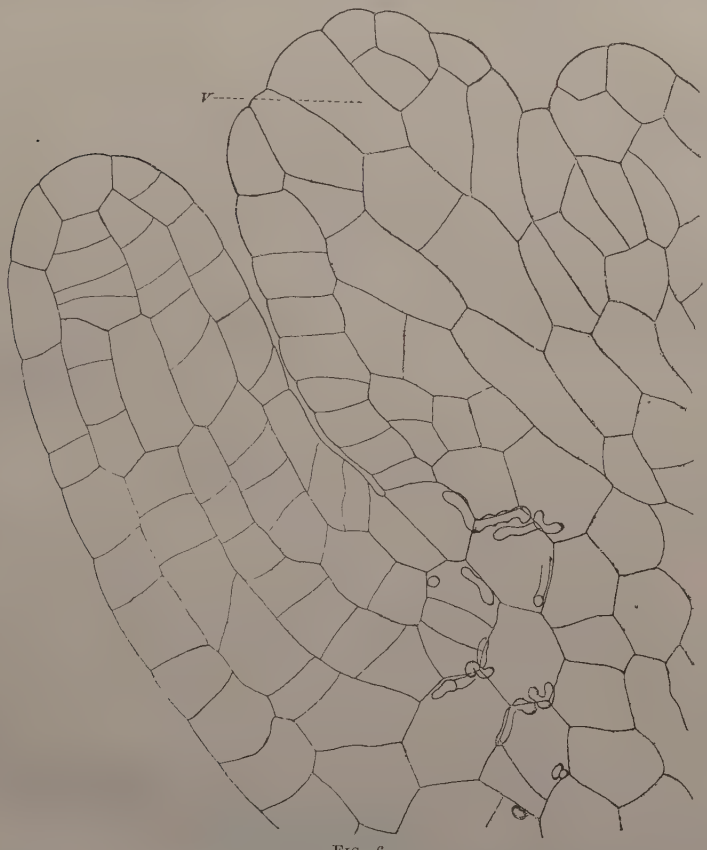


Fig. 6.

experiments have also been carried out by the United States Department of Agriculture, and in a communication, dated October, 1908, it is stated that "During the last two years numerous inoculation experiments have been performed with the loose smuts of wheat (*Ustilago tritici*) and loose smut of barley (*Ustilago nuda*). In the case of both of these smuts infection takes place only at the time of flowering of the host. The smut spores are easily carried by the wind, and as the wheat and barley glumes open for a short time during the process of pollination, the spores readily gain entrance and infect the developing ovary. The smut-germ then lives intraseminally until the grain sprouts in the spring, after which it grows along with the host, and at flowering-time becomes evident as the well-known loose smut."

4. Shoot Infection.

The only method of infection recognised for a long time among the smuts was that of the seedling being attacked by the germinating spore attached to the seed, and this was known as *Seedling infection*. Next it was found that in American corn smut young and growing portions might be attacked,

and this was called *Local infection.* Then it was discovered that the young ovary or other portions of the flower might be infected by the germ-tube of the spore producing in some cases a mycelium inside the seed, so that when the ripe seed was sown next season, the resulting plant was diseased. This is known as *Flower infection* and occurs in *Ustilago tritici* and *U. nuda.*

Next Hecke[1] discovered a fourth mode of infection, which he called *Shoot infection,* and it was suggested by what occurred among the numerous Lychnis plants which had been grown from seed obtained from the flowers that had been infected. Such seed produced nothing but sound flowers in the summer, but one plant formed a smutted flowering shoot in October (autumn). There were, at least, two possible explanations of this. It might be accounted for by flower infection, the summer flowering shoots escaping by their rapid growth, while the fungus reached the growing point of the more slowly developing autumn flowering shoot, or there was the possibility that the plant was originally sound and was subsequently infected by neighbouring diseased plants grown in pots alongside. Such an infection could only be conceived to take place by the mass of spores falling to the ground, germinating there, and producing their conidia, which reached and infected the young shoots arising at the collar or top of the root. In order to prove this possibility, he experimented with perfectly sound two-year old plants of *Lychnis alba.* They were grown from seed in pots and cut back in October as far as possible to the collar or the portion level with the ground. Then the exposed collar was dusted with spores of *Ustilago violacea* and covered with manure containing similar spores. A few weeks afterwards the freshly formed shoots appeared at the surface, and in May of the following year began to flower. The flowers produced were smutted and their diseased condition can only be referred to the shoot infection which took place in October.

The Anther smut (*Ustilago violacea* (Pers.) Fckl.) is able to produce its spores only in the anthers or male organs. This fungus infects the Campion (*Lychnis dioica*) which has the sexes on separate individuals, and it not only attacks the male plant where the anthers are normally developed but also the female plant which normally never bears them. In the male plant it produces its violet spores in the anthers naturally present, but in the female plant it still produces its spores, although anthers are absent in the natural condition. It stimulates the female host in some way to the production of stamens in which it may develop its spores, while the pistil normally developed, is suppressed. The fungus is evidently able to induce the conditions necessary to the formation of male organs, although elaborate experiments by Strasburger failed to produce this effect in uninfected plants. We must assume that both sexes exist, but the dominant one only becomes visible while the other remains latent, and this dominance may be controlled by an internal stimulus which may influence the particular kind of nutriment available. Change of sex is here shown to be possible, but how it is brought about cannot be definitely stated, further than that it is determined by internal, not external factors, and since it is the young shoots which are infected, the sex may be determined long before the appearance of the flower.

A similar experiment was made with *Urocystis occulta.* The perennial *Secale montanum* was employed as a host-plant, after it had been shown that plants of this species, which were cultivated in gardens, became naturally infected by *Urocystis occulta* produced upon the rye (*Secale cereale*). In this experiment all shoots were likewise cut back to the collar and then infection was made in the autumn with spores and manure containing spores. The result was that in the spring of the following year, the shoots produced were smutted.

Dr. Hecke comes to the conclusion from these experiments "that besides the seedling and flower infection, there is still another kind of infection among smuts, that is to say, shoot infection. It is probable that this kind of infection occurs not only with *Ustilago violacea* and *Urocystis occulta*, but also with other smuts as well. The smuts of perennial plants are especially considered here, but it is possible that the same thing occurs in the case of infected shoots of cereals. A series of experiments of this kind is being carried out with different smuts, the results of which will be given later."

This will account for the infection of the shoots of cereals by *Urocystis occulta* or flag smut, by these young and tender shoots coming into contact with the diseased straw and other spore-bearing material in the soil, in the process known as "tillering." When the primary or terminal bud has about reached the surface of the ground, then lateral buds may be formed in the axils of the leaves about the same position. These lateral buds or "tillers" as they are sometimes called, usually develop into branches, and these branches may in turn produce other branches, so that from a single grain of wheat a plant may be developed consisting of numerous stalks each bearing an ear. Such an individual plant with numerous stems arising from a common root is usually called a "stool" and the process by which the plant thus adapts itself to its environment is known as "stooling" or "tillering." This branching takes place at the joints or nodes near the surface of the ground and as many as 125 stalks of Steinwedel wheat with 125 perfect ears, with an average of fifty grains in each ear have been recorded and photographed by Thompson[1] in New South Wales. It is evident that the smut fungus may enter these numerous stalks, either by directly infecting the young seedling, or by gaining an entrance through the young shoots, or, as in the case of plants living more than one year, by a perennial mycelium.

The case already given of a smutted barley plant being cut back and the fresh shoots being again infected by the mycelium persisting in the lower nodes, shows that we have to distinguish between infection of the shoots from without and from within.

Collection of Spore Material.

For successful infection it is necessary to have the material as fresh and as well preserved as possible and taken direct from the fields where it is produced. To preserve it in the best possible condition for the following spring requires care and attention, for if special precautions are not taken, it may be injured by moulds or by grubs so as to be quite useless. To guard against such injurious influences, Brefeld adopted the following method of collecting and preserving plenty of pure spore material as the result of a lengthened experience. It should be gathered in sufficient quantity soon after the exposure of the spores, before grubs or moulds can gain access to it and preserved for about a week in a dry place. Then the spores are passed through a fine sieve on to white paper and the residue is thrown away. The result is that the spores which have passed through the sieve are in a powdery and dry condition, and keep well until the next spring. The spores are next placed in small tubes, only filling them to about a quarter of their capacity, and the neck is securely closed with sterilized paper before laying them aside in a cool dry place during the winter. A number of these tubes are filled, so that if some should happen to deteriorate, the others may be perfectly pure.

Just before using the spores in the spring for the infection of the young seedlings, they were placed in pure water and thoroughly stirred up in the centrifuge. This treatment of the spores and leaving them to settle for one day in the water, not only cleaned them thoroughly but rendered them most

favorable for germination, and when placed on the young seedling in dilute nutritive solution, they germinated without loss of time and directly produced infection.

In the case of stinking smut of wheat, there is no difficulty in securing well preserved material. The unbroken smut-balls are filled with the uncontaminated spores and require only to be crushed in order to dust the grain to be infected.

The Influence of Temperature on Infection.

Brefeld[4] came to the conclusion, as the result of experiments with oat smut, that a low temperature at the time of germination favours successful infection, so that sowing in the spring, when a higher temperature than in winter usually prevails, is less favorable to it. But Tubeuf[2] and others proved quite the contrary, that a high temperature brought about a higher degree of infection, and they recommend late autumn sowing as a means of reducing the amount of smut.

On the other hand, it has been proved by carefully conducted experiments, that in the case of stinking smut of wheat, sowing late in the autumn, when the temperature is low, encouraged it, other things being equal. In all these experiments, however, it must be borne in mind, that neither temperature nor infection ought to be considered independently, but that there are modifying factors which must be taken into account. Thus rapidity of germination and a quick growth, will counteract the effects of temperature, for if the fungus cannot keep up with the rapidly elongating plant and reach the growing point, the host-plant will remain sound, in spite of the temperature.

Hecke[5] has considered the influence of temperature in its threefold aspect of—1st. Effect upon the germination of the spores and the seed grain; 2nd. Upon the duration of the infective stage of the host-plant; and 3rd. Upon the possibility of the fungus reaching the growing point of the host-plant.

1. If the temperature of germination be compared for the fungus and its host, it is found that in wheat the minimum is practically the same for both. For the wheat it is 3–4.5° C., and for the spores of stinking smut, 5° C., so that, usually, the wheat and the spores will germinate together. But in the case of oats, there is a considerable difference. The minimum temperature for the germination of oats is 4–5° C., while the spores require 5–11° C., hence the oat itself may germinate at a low temperature while the spores remain stationary.

2. Cold and damp weather tend to retard growth, so that the infective stage is prolonged, and at the same time, the tissues being soft and tender, infection is rendered more certain.

In the stinking smut of wheat, the principal effect of a low temperature consists in lengthening the period during which infection is possible, for the spores and the wheat, germinating together, along with the retarded growth, will insure the fungus filaments inside the plant reaching the growing point.

3. Since our wheats are all sown in the autumn or early winter, there is little rapid growth at first as a rule, so that the fungus has sufficient time to reach the growing point and establish itself in the host-plant. But it is in the summer wheats that the influence of temperature is most marked in favouring or hindering the fungus in reaching the growing point, and this may account for the great variety in susceptibility shown by such wheats towards the stinking smut.

It will now be clearly understood why a low temperature at the time of sowing, especially if the soil is damp, will be favorable to the infection of wheat by stinking smut, while in the case of oat smut it will be rather the reverse, since it retards the germination of the spores.

The different results obtained by Brefeld and Tubeuf in connexion with oat smut may be explained from the fact that Brefeld used germinating conidia mixed with earth in which oats were planted, while Tubeuf used conidia which had not germinated. In the one case the low temperature was applied after the spores had germinated and it was assumed that in the slowly developing seedlings, owing to the cold, the fungus had penetrated to the growing point, and this produced a high percentage of smut. In the other, the pots were placed in a low temperature during the germination of the spores, with the result that the oats germinated, while there were very few spores to infect them.

Whatever hinders the rapid development of the seedling and extends the period of infection, will favour the access of the germ-tubes of the germinating conidia to the growing point.

CHAPTER VII.

Smuts in their Relation to Rusts.

It has always been more or less generally taken for granted that there is some sort of relation between the rusts and the smuts, but the exact nature of that relation has never been definitely settled. On a superficial view, there are seen to be black masses of spores produced in both cases, often bursting through the particular parts of the plant on which they occur, which suggest some close connexion, and even the farmer has been misled by this superficial resemblance, for he invariably calls flag smut of wheat (*Urocystis tritici*) "Black rust."

On closer and deeper investigation, they are still found to have many points of resemblance, so much so, that both were placed together by the older writers under Fries' division of the Hypodermii. At the present time Brefeld[8] who has studied the smuts more thoroughly than any other living investigator, regards them as the progenitors of the rusts, and this genetic connexion is supposed to be proved by various structures which they possess in common. There was one jarring note, however, introduced to disturb the harmonious relations which were supposed to exist between the two, and that was by De Bary, as early as 1853. He considered that the rusts were very closely allied to the Ascomycetes, while the smuts were more nearly related to the Phycomycetes, but in order to understand the points of difference, as well as the points of resemblance, it will be necessary to make a general review of the position.

There are three primary groups of fungi still generally recognised, which are based upon purely morphological characters. The Phycomycetes or Alga-like fungi are regarded as the primitive stock, and divergence has taken place in two directions, the offshoots representing the other two main divisions. The Ascomycetes are characterized by the ascus containing a definite number of spores, and the Basidiomycetes by basidia or large terminal cells bearing naked spores at their free apex.

Brefeld[8] has pointed out that, in the Basidiomycetes there are two different forms of basidia. In the one case, the basidia are septate, and a spore arises from each cell, while in the other, they are undivided and bear at the apex a definite number of spores, usually four. The most primitive forms of basidia are divided transversely, hence called Protobasidia, and the undivided basidia are known as Autobasidia. In the smuts, the promycelium arising from the spore agrees with the divided basidium of the Proto-basidiomycetes, but there is nothing corresponding to the undivided basidium of the Auto-basidiomycetes, when fully developed forms are taken into consideration. There are still some who strain analogy so far as to make the promycelium of the Tilleticae correspond with an undivided basidium, but the septa or divisions are just as pronounced in their promycelia when mature, as in any of the Ustilagineae. The promycelia of the smuts are, therefore, regarded by Brefeld as primitive basidia, foreshadowing the special basidia of the Basidiomycetes, and the only point of difference between the two consists in the promycelia of the former bearing a variable number of conidia, while the basidia of the latter bear a definite number. The smuts are therefore called by Brefeld Hemibasidii, forming a sort of half-way house to the Basidiomycetes proper, and they show their primitive nature, like the rusts, by representing the type in which the basidia are still divided. The Tilletieae,

however, show a step in advance by the characteristic whorl of conidia at the apex of the jointed promycelium.

According to this view, the smuts have given rise to the Basidiomycetes and form the connecting link with the Phycomycetes. But there are others, such as Moeller and Massee, who assign a different origin to the Basidiomycetes, the latter regarding them as having originated independently from conidial forms of the Ascomycetes.

Having shown that the smuts are, probably, most nearly allied to the primary group of the Basidiomycetes, let us now see in what relation they stand to the rusts. The smuts are all parasitic fungi, mostly occurring in the tissues of the higher plants, more particularly in the Gramineae, which are often seriously injured by them. The spores are produced, as a rule, in the interior of special or *sporogenous* hyphae, the walls of which become gelatinous and finally deliquesce, while the protoplasm in the interior, develops into the spores. When the ripe spores are thus set free, they germinate under the influence of moisture, after a longer or shorter period of rest, or immediately. The outer coat of the spore bursts at a particular spot and a germinal tube is protruded, which ultimately divides by means of transverse septa into two or more cells. As in the case of the rusts, this germinal tube is called a *promycelium*, and it bears the spore-like bodies or *sporidiola* here called conidia.

De Bary regards this germinal tube as of the nature of a mycelium, while Brefeld considers it a basidial structure, and if we accept this latter view, then the smuts, as well as the rusts, are akin to the Basidiomycetes. The whole question turns upon what is meant by a basidium. A basidium is generally considered to be a relatively large cell giving rise at its apex to a definite number of naked spores, which are produced only once at fixed spots. It must be granted at once that the germinal tube or promycelium in the smuts has not the definite characters of a true basidium. It is divided into several cells, conidia may be produced laterally as well as terminally, and when they fall away, new ones may be produced. But it may well be regarded, in its most primitive form, as a transition stage to the more definite characters met with in the rusts. In the rusts there is a definite promycelium, consisting of four cells, and each cell bears a single conidium or promycelial spore, which is only once produced, although Brefeld[8] has shown that the conidia in the smuts may sprout and produce secondary and tertiary conidia in a nutritive solution. It may be considered as the variable form from which the definite rust form has arisen.

Not only was the product of the spore different from that of the rusts, according to De Bary, but he pointed out that the smuts were essentially different in the mode of formation of their spores. There, the contents of the hyphae at certain definite spots are transformed into spores and the walls of the sporogenous hyphae deliquesce and set them free, while in the rusts the spores are pinched off from the ends of the hyphae. No doubt, this is a distinct difference, but when the sexuality of the rusts is considered and the spores are seen to be the result of this, then a different mode of formation was inevitable.

But perhaps the most important difference between the two, according to De Bary[3] is the conjugating cells. He writes :—" If, on the other hand, we look for the points which are distinctly characteristic of the Ustilagineae, the most prominent is that of the conjugating pairs of cells." He considers the pairing of the promycelial spores or conidia as of the nature of a sexual act, but it is not now regarded as such, according to the present state of knowledge. It is simply a means of mixing the protoplasm from two different sources, through anastomosis and occurs in germ-tubes and hyphae as well. This brings us to the question, however, of true sexuality in both. I have

already called attention in my work on "The Rusts of Australia," to the discoveries of Blackman and Christman, showing that there are true sexual cell fusions in the aecidial stage of the rusts, and this has been extended to forms possessing uredospores and teleutospores by Olive[1] and others. Dangeard[2] has also shown that when sexual reproduction, as he considers it, is about to take place in the smuts, the cells concerned become swollen. Each single swollen cell contains two nuclei, and the fusion of these two nuclei to form one is regarded as an act of fertilization. But this is not the kind of fertilization which occurs in the rusts investigated, and it will be necessary in order to understand clearly the relation between the two, to give a brief life-history of both.

In the rusts the condition in which two nuclei occur in a cell is shown to arise in aecidia in the fusion cells or "basal cells," so called because they subsequently give rise to the chains of æcidiospores. The binucleate basal cell is the result of the conjugation of two uninucleate cells, so that the contents of two distinct cells enter into its composition. The nucleus, together with the protoplasm of one cell passes into the other cell by means of a pore in the wall separating the two cells, and the latter or receptive cell is thereby fertilized. These sexual cell fusions may either represent true sexual reproduction, in which the two uniting cells are clearly distinct like the ovum and sperm, or the two uniting cells may show no appreciable differences. The former, is called by Winkler,[1] *Amphimixis* and the latter *Pseudomixis*, so that we have here an instance of Pseudomixis, for the two fusing cells, as well as their nuclei, are approximately equal.

The mycelium which bears the uninucleate fusion cells has also single nuclei, but the product of the fertilized cell is a growth with paired nuclei. Hence all the constituent parts of the spore-bearing generation or *Sporophyte* show in their cells the paired nuclei, including the aecidiospore, the mycelium arising from them, the uredospores, and teleutospores. When uredo- and teleutospores only occur, they originate from similar fusion cells, and Olive has investigated a species possessing only teleutospores, and found that the binucleate condition arises in the basal cells, which give rise to teleutospores almost immediately.

The mycelium in the host-plant, bearing the sexual cells or gametes which are all uninucleate, constitutes the *Gametophyte*. There are thus two distinct stages of the rust starting in each case from a single cell. The fertile cell is the starting point of the spore-bearing generation or Sporophyte, and the spore is the beginning of the sexual generation or Gametophyte, and there is a regular alternation of the sexual Gametophyte and the asexual Sporophyte.

In the smuts, on the other hand, only the asexual generation is represented, and the single spore corresponds generally to the teleutospore of the rusts. The mycelium has two nuclei in each cell, at least when young. In certain swollen cells the two nuclei already contained in the cell combine and fuse to form one, and it is this nuclear fusion within the one cell which Dangeard considers sexual reproduction. It may also be remarked that in the rusts the two nuclei finally fuse in the teleutospore as it matures. But it is of the essence of the sexual process that the nucleus passes from one cell, representing the male, to the female receptive cell, and it is just here that the difference lies between the origin of the spore in the rusts and the smuts. The binucleate swollen cell which becomes the spore in the smuts is not connected in any way with a sexual process, while the spore generation in the rusts is the result of sexual cell fusion.

The smut spore otherwise, generally resembles the rust teleutospore in the product of its germination. It produces a 3-4 celled filament bearing conidia,

but these conidia are not definite in number and may be produced more than once from the same cell. This multiplication of the conidia seems a necessary consequence from the fact that there is only one kind of spore. The conidia may either directly germinate and produce the sporophyte, or they may multiply in a yeast-like fashion before doing so, according to the supply of nutriment. The yeast-like budding of the conidia not only multiplies the means of reproduction, but carries the fungus over the period when no host-plants are available. The germination of the teleutospore in both rusts and smuts does not always result in the production of a promycelium. In the rusts every gradation may be observed from the ordinary germ-tube as in aecidiospores and uredospores to the special conidia-bearing promycelium. Its mode of germination evidently depends largely on surrounding conditions. Fischer[2] observed this in Gymnosporangium, where conidia were only formed in air, while in water an elongated germ-tube was produced, and Magnus[1] has repeatedly observed that when the teleutospores of *Puccinia graminis* were germinated in water, they produced a germ-tube just like that of a uredospore. The teleutospore in the rusts has therefore departed from the ordinary mode of germination of producing a germ-tube which directly infects the host-plant, but multiplies itself by means of minute conidia suited for aerial conditions, and giving rise in the host to a mycelium which bears the sexual cells. The production of conidia, too, outside the host-plant will also have an invigorating effect when they are nourished in a saprophytic manner. Brefeld[3] cultivated the conidia of rust fungi in a nutritive solution, and found that they budded so as to form secondary and tertiary conidia, and in smuts this mode of nutrition has produced the most luxuriant budding. While in the smuts the spore produces generally a promycelium bearing conidia, there is frequently only hyphae, and in infection through the flower it is the rule for the spore to germinate direct and form a mycelium.

If we compare the life history of a smut with that of a rust there is seen to be partial resemblance, with important differences such as the absence of a sexual stage. There is sufficient resemblance, however, to indicate some affinity, and the question is as to the nature of it.

As to the origin of the smuts, we can only arrive at a reasonable conclusion by taking all the facts into consideration and comparing them with others, seeking to find a place in the general scheme of life where they best fit in, and associate them with those forms with which they are most in agreement.

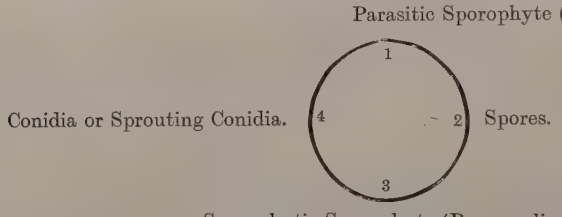
Brefeld regards them as having been derived from the Phycomycetes, and as this group possess both sexual and asexual forms of reproduction, they are supposed to have originated from the latter. He also lays a great deal of stress on the fact that the spore on germination produces what he considers a basidium, and since the rusts also give rise to a similar structure, more definite and more nearly approaching the type, he regards the smuts as the precoursors or progenitors of the rusts, and through them of the whole group of Basidiomycetes. But, as we have already seen, there is room for difference of opinion as to the origin of the Basidiomycetes, and consequently of the relation of the smuts to them.

My own idea is that the *Ustilagineae* may be simply regarded as forms which have a distinct alternation of a saprophytic with a parasitic stage, and with sexuality grafted on to this, they originated the *Uredineae*. It is considered that the promycelium bearing conidia is a saprophyte, because it generally grows freely in a nutritive solution

It is now generally accepted that all fungi were originally saprophytes, living upon dead or decaying vegetable matter, and that some of them gradually became accustomed to a parasitic habit. The division of fungi into saprophytes and parasites is convenient, but not natural, for there are

saprophytes which are occasionally parasitic, and parasites which are occasionally saprophytic. In the case of grey mould (*Botrytis*) and blue mould (*Penicillium*) we see parasites in the making, as it were, for they are able, under certain conditions, to enter the living plant and grow there as ordinary parasites. It is not so well known, however, that there are also true parasites, which spend a portion of their existence outside the host-plant, and, not only so, but saprophytic and parasitic stages regularly alternate in their life-history.

The smuts were originally entirely *saprophytic*, and this stage is still represented of course in a much reduced form in the promycelium bearing conidia. The promycelium is all that remains of what was once probably a much more elaborate organism. Next, they became educated up to and developed into the *parasitic* stage, and this gradually took the lead, until now it is the most conspicuous form, and is represented by the internal mycelium bearing spores. Only one kind of spore is produced, but by means of nuclear fusion, which serves the purpose of a sexual act and foreshadows it, it is invigorated and rejuvenesced. There is here an alternation of a saprophytic, with a parasitic stage, and it may be represented graphically thus :—



The earliest alternation was that of nutrition, as represented by a saprophytic and a parasitic mode of life, and this gradually developed into an alternation of spore-forms, using the term spore in its widest sense. The parasitic form ultimately developed into a sexual form, so that an alternation of a sexual with a non-sexual generation arose.

With the development of sexuality a higher plane was reached, and greater variety in the reproductive bodies secured, each specially adapted for different conditions, and ultimately for different host-plants. This was the starting point of the new group of rusts. It is interesting to note, in this connexion, that Christman holds that the teleutospores are the primitive spores of the rusts, and that the other kinds have been gradually intercalated in their life-history. There is here, as in higher forms, a distinct alternation of a sexual and asexual stage.

The *sexual* stage is represented by an internal mycelium bearing sexual cells or gametes, the contents of which blend and produce the fertilized cell.

The *asexual* stage is the product of the fertilized cell, and is represented by the aecidisopores with their intercalary cells, and the mycelium produced by them bearing uredospores and teleutospores. This is the *parasitic* form of the sporophyte, which sometimes completes the cycle by the teleutospore directly infecting the host-plant and producing a mycelium bearing the sexual cells.

But, generally, the *saprophytic* form of the sporophyte asserts itself, by the teleutospore producing a promycelium bearing conidia, and the conidia infecting the host-plant.

The alternation of generations in the Rusts may be thus graphically represented :—

In both smuts and rusts there is a tendency to dispense with the saprophytic stage, and become more perfect parasites, as, for instance, in the species of smut infecting the host through the flower, and *Puccinia graminis* in Australia dropping this stage altogether.

Alternation of Parasite and Saprophyte.—Only one kind of reproductive body is formed inside the host-plant, and these smut spores are produced by the parasitic form of the fungus. When these spores are set free and scattered by the wind or other agency they may either immediately, or after a period of rest, begin to germinate. This process of germination takes place outside the host-plant, and gives rise to a promycelium which generally produces conidia, either laterally and terminally, or only at the apex. Germination readily occurs in a nutrient solution, and since the formation of conidia has been carried on by this means from generation to generation for more than a year, as in the oat smut, this must be regarded as the saprophytic form of the fungus. In some instances, as in Tilletia, when food material is abundant, the promycelium is not limited to a short germinal tube, but grows into a large branched mycelium like a tuft of mould, which bears conidia, differing slightly from those produced normally. While in the rusts two different host-plants are often concerned, in the smuts there is only one, but a saprophytic mode of life succeeds and alternates with the parasitic mode of life. During the parasitic stage, there is a definite form of spore produced which is capable of giving rise to conidia on a germinal tube, and in the saprophytic stage the conidia formed are capable of sprouting continuously, as long as the nutriment lasts, and then putting forth a germ-tube which penetrates the living plant if it comes in contact with it at the right stage. In the one case the living and the dead substratum exerts an influence which results in the different reproductive bodies, in the other it is the living substratum of different host-plants which produces the variety of spore forms. The researches of Klebs[1] already referred to, show that it is just this exhaustion of food in the successive host-plants attacked which brings about the different reproductive bodies.

The rusts have an advantage over the smuts in the variety of spores produced, and their appearance at different seasons of the year. Not only have they reached the highest degree of specialization in the selection of their host-plants, often confining their attention to one particular species, but they may select one plant for the production of spring spores and another for summer and winter spores, so that their distribution is increased and their adaptation to varying climatic conditions improved.

Aecidia-like Forms.—In the higher forms of smuts there is an approach to the aecidia of the rusts, and the characters of Doassansia and Cintractia are very suggestive in this connexion. In Doassansia the fertile spore-clusters are enclosed in a peridium formed of closely packed sterile cells, arranged in a single layer. In Cintractia the spores are developed in rows,

the older and more mature being on the outside, and they are often contained in a special receptacle formed by several layers of sterile cells. So striking is the resemblance that Brefeld asserts that if the characters of the two genera were united in one form there would be almost complete agreement with the aecidia of the rusts, and he considers it not improbable that such forms may yet be discovered. In such a case the smuts might reasonably be regarded as the progenitors of the rusts, the primary forms from which they were derived.

If we sum up the principal resemblances and differences between the smuts and the rusts, it is found that they agree in the following :—

1. They are all parasites.
2. They produce a promycelium bearing conidia.
3. A peridium is sometimes present, and spores are produced in a radiating manner resembling an aecidium.

And they differ :—

1. In the promycelium producing a variable number of conidia.
2. In the promycelium of some species growing and branching in a vegetative manner without the formation of conidia.
3. In the mode of production of spores, which are formed in the interior of the hyphae and not pinched off at their apex.
4. In the production of one spore form, and not a variety.
5. In the absence of a true sexual process.

CHAPTER VIII.

Parasitism and Immunity.

In connexion with the diseases of plants, where fungus parasites are concerned, determined efforts have been made to study these parasites in such a way that their life-histories might be made out, and their mode of infecting the host-plant and producing the disease thoroughly understood, the object being, from the knowledge thus obtained, to prevent the parasite gaining an entrance into the host. This has hitherto been usually accomplished, either by destroying the spores of the fungus or preventing their germination, and thus effectually preventing the appearance of the disease. By means of spraying, for instance, at the proper time with suitable fungicides, a large number of such diseases have been kept in check, and so successful had this method proved that the hope was entertained by many that it only required a further extension of our knowledge of plant parasites and their life histories, in order to completely overcome their destructive effects. This was a great step in advance, even although it involved unceasing warfare against the parasite, and the Department of Agriculture of the United States of America led the way in demonstrating the efficacy of the gospel of spraying.

But there were some serious diseases due to parasitic fungi which did not lend themselves to this mode of treatment, even although the history of the parasite had been followed from spore to spore, and it became necessary to devise other means for controlling the disease. Foremost among these was the Rust in Cereals, to which, from the very nature of the mode of attack of the parasite, and the manner of growth of the host-plants themselves, it was found to be mechanically impossible to apply this method of prevention.

It will be observed that in this method of grappling with disease, the host-plant itself is left out of account, and attention is concentrated on the parasite. But there is another possible way of preventing disease, and that is by rendering the plant immune. Accordingly, attention was turned to the question of immunity or resistance to disease, which has been for some time deeply studied and discussed in connexion with human diseases, and which has also been observed in some species and varieties of cultivated plants, such as wheats and other cereals. The definition of an immune plant as given by Massee[3] may be accepted. It signifies an individual of the same species as the one on which a given species of fungus is parasitic, but which, owing to the absence of the chemotactic substance in its tissues necessary to enable the germ-tubes of the fungus to penetrate, remains unattacked. Only it is to be understood that while the parasite may gain an entrance, it does not normally develop in such an "immune" plant, and, consequently, cannot produce the harmful disease or spread infection by means of its spores.

In dealing with the smuts with which we are more immediately concerned, there were various steeps for the seeds, or disinfectants, as they may be called, such as sulphate of copper or bluestone, and formalin, which effectually prevented the attacks of some of the more common smuts, but there were others, such as the destructive flag smut of wheat, which did not yield to such treatment, and even here it is becoming apparent that immunity to the disease is to be aimed at as a means of overcoming it. In short, at the present time, it is felt that our present methods of fighting parasitic fungi is simply tinkering

with the disease, affording only temporary relief, and that the only permanent and natural means for overcoming them lie in following Nature's methods for preventing extinction of the species, by rendering the plants themselves immune, or at least, partially immune to such attacks. Before this goal is reached, numerous researches in the laboratory and experiments in the field will require to be carried out, but already there are sufficient instances known to justify our hope and that of Rust in Wheat may be taken as an example.

Rust Immunity.

There are, at least, three different kinds of rust which attack wheat, the Black Rust (*Puccinia graminis*, Pers.), the Brown Rust (*P. triticina*, Eriks.), and the Yellow Rust (*P. glumarum*, Eriks. and Henn.). Only the two former occur in Australia, and it is the so-called Black Rust which is so injurious in certain seasons, while the Brown Rust is comparatively harmless. It appears that in Britain and America the Yellow Rust does considerable damage, and it is this one which has recently been made the subject of exact experiment. Mr. Biffen, of the Agricultural Department of Cambridge University, found in his plots a strain of wheat which was immune to this rust, for although under observation for four seasons, and surrounded by varieties susceptible to the disease, it remained free and showed no trace of infection. This wheat belonged to the sub-species, *Triticum compactum*, or Dwarf Wheat. On the other hand, there was a type known as Michigan Bronze which was so liable that not a single individual escaped, and comparatively few ripe grains were obtained. On crossing these two types, the first generation consisted of plants badly rusted without exception, even the awns and grains being affected, but fortunately, a number of ripe grains were obtained for subsequent sowing. Every available grain was sown to produce the second generation, in plots alongside the parent varieties. The result was that while every individual of the susceptible variety was infected and the immune variety escaped entirely, the crosses were badly rusted, but certain individuals stood out perfectly clean, not showing signs of disease, even on the withering basal leaves. The second generation of the cross was thus composed of plants either badly rusted or immune, and the exact numbers were 1,609 diseased and 523 immune, or a ratio of 3.07 to 1.

Biffen has found another wheat which possesses an even greater degree of immunity to Yellow Rust than the American Club—the variety of *Triticum compactum* already referred to. It is known as Einkorn, or *Triticum monococcum*, and is said to be exceptionally immune to the three common rusts.

There is a principle here which is found to hold for diseases other than rust, and it opens up great possibilities in the way of breeding plants immune to disease. There are certain varieties of wheat, for instance, which are more or less immune to rust, but lacking in those useful qualities which the farmer desires, such as strength of straw, holding of grain, prolific yield, &c. But when it is discovered that these unit characters, as they are called, go in pairs, such as susceptibility and immunity to rust, and that they can be combined with other characters which obey the same law, by crossing, then it is seen to be possible in three generations to obtain a pure strain by crossing, combining these desirable qualities with immunity to rust. If two fixed strains are crossed, all the possible forms obtainable appear in the second generation if a sufficient number of plants are grown, and a certain proportion of each of these forms is already fixed. The third generation will show those individuals

which are fixed, and breed true, and thus two generations are sufficient to produce and fix the new variety. There is also a definite proportion between the fixed and unfixed sorts. In the particular instance given, where two contrasted characters are concerned, the susceptibility to rust is called the *dominant* character, because it prevails over the other or *recessive* character in the first generation, and this holds good irrespective of which plant was pollen-bearing or seed-producing. In the second generation, the dominant "rusty" plants and the recessive "immune" plants appear in the ratio of 3 to 1, as nearly as possible.

Smut Immunity.

Although I am not at present (1909) in a position to give such definite results for smut as have just been given for rust, yet experiments are under way to settle the point as regards Stinking Smut, or Bunt. The difficulty here is to secure wheat-plants which are immune to this smut when grown under conditions favorable to its development, such as the seed-wheat being dusted with the spores, but this difficulty is being gradually overcome.

There is a variety grown here, known as Allora Spring, which is most susceptible to bunt, having yielded 95.5 per cent. of bunty plants when the seed was coated with spores, while under the same conditions, Minnesota Blue Stem, a strong flour variety, was the least susceptible of ten varieties tested, only producing 12 per cent. But while a small proportion of rust is admissible without seriously interfering with the yield or the quality of the grain, a very small percentage of Stinking Smut is objectionable, and it is necessary, if treatment of the seed is to be dispensed with, to have a variety or strain which is absolutely free. Experiments in the direction of producing bunt-resisting wheats have been hitherto mainly carried out by Farrer and Pye. The work of Farrer is being continued by Sutton at the Cowra Experiment Farm.

Experiments of Farrer and Sutton in New South Wales.

When the grains of different varieties of wheat are thoroughly dusted with bunt spores and sown at the same time alongside each other, it is found that the percentage of bunty plants varies considerably according to the variety, basing the calculation upon the number of plants which grew in each case and not upon the number sown. Thus, in experiments carried out by Farrer[3] with ten different varieties, the percentage varied from 95.5 to 12, and the proportion which remained clean might be owing to the fact that either the plants themselves, or the seeds from which they grew, possessed the property of resisting infection. But there are various other causes which might produce this result, even on the assumption that the bunt spores germinated, such as germ-tubes which penetrated the seedlings failing to reach the growing point, or the growth being too rapid for the mycelium to keep up with it. So that the only way to settle the point was to harvest the clean plants separately and sow the seed after inoculation, in order to see whether any of them transmitted the quality of bunt-resistance to their progeny. This was accordingly done with different strains of Allora Spring, and the lowest percentage of bunty plants was 87.1, and the highest 95.5. While carrying out these experiments, Farrer hit upon the idea of selecting clean plants from the strains of his crosses which showed the smallest percentage of bunt, in order to see if bunt-resistance could be increased by a course of systematic selection. He observed that the plants of the variable generation of a cross differed widely in their liability to bunt, just as has been observed in the case of rust, and he came to the conclusion that if the plants of this generation were exposed to infection,

by inoculating the seed from which they were grown, then a large proportion of the plants which might otherwise have produced bunt-liable varieties would be culled out, and a higher average of bunt-resistance would be secured in those retained. And if the next generation was also similarly infected, further culling-out could be made and a still higher average of bunt-resistance secured in the remaining plants.

In 1901, experiments were begun in inoculating with bunt the seed which produces the variable generation of new crosses, and in reporting on these Farrer[9] remarks :—"A large number of experiments were made in sowing bunt-infected seed of unfixed and partially fixed crossbreds, with the object of seeing into the possibility of making varieties which are valuable on account of the resistance they offer to the infection of bunt. No good purpose would be served by describing these experiments in detail. The results, however, from sowing seeds produced by plants of the variable generation which were free from bunt in 1901 are exceedingly encouraging, but it remains to be seen whether and to what extent these good results are due to the exceptional character of the season." And in his report for 1903[10] he states :—"Whether bunt-proof varieties will ever be secured is, of course, as yet uncertain ; but I have on hand some newer crossbreds which promise to yield varieties which are better resisters of this parasite than are any of the first batch." And in 1905[11] he writes :—"The investigation, however, is very laborious and will take a longer time than I am likely to live. That I am now in a position, however, to select bunt-resisters as parents for crosses is in the direction of helping matters on. Crosses for the special purpose of securing bunt-resistance were made this last season (1904) for the first time."

The lamented death of Farrer, on 17th April, 1906, deprived us of the benefit of his scientific skill and ripe experience, but Sutton[2] has brought to fruition the experiments which he initiated. The result is that he has succeeded in producing varieties which apparently resist bunt, for he writes as follows in the *Agricultural Gazette* of New South Wales for March, 1908 :—"Florence and Genoa have, in our trial plots, shown themselves, under severe trial, to be practically smut-proof, and in consequence, seed of them does not require to be blue-stoned or treated with any other fungicide for the prevention of smut." Florence and Genoa are the result of the same crosses, the parents being White Naples, Improved Fife, Hornblende, and an Indian wheat. Although only different strains of the same breed, they vary in the period of ripening, Florence being very early and Genoa about a fortnight later. Genoa also stools much more freely than the other with us. The method followed was to inoculate as thoroughly as possible the seed of each generation of the cross and in this way to arrive at the most bunt-resistant. "Florence and Genoa have proved themselves to be over 99 per cent. smut-resistant, that is to say, that out of 100 seeds thoroughly infected, ninety-nine plants have been found to be entirely free from smut at harvest time." That is certainly a very good record and justifies the hope that the treatment of the seed for the prevention of smut may yet prove unnecessary ; but in order to command full price, the wheat must be, as near as possible, bunt-free. In order to get an idea of what the trade required, I communicated with one of the largest dealers in wheat, and received the following reply :—"When selling wheat, we do not allow any percentage for smut. It entirely depends on the condition of the wheat ; if the smut balls are not broken and the wheat not much contaminated, it will probably be about 1d. per bushel under prime wheat ; but if the balls are broken and the wheat badly smutted, the difference is often from 6d. to 9d. per bushel." If the market rates are taken as a guide, there may be from 6d. to 1s. deducted per bushel on account of smut. When good milling wheat

was selling at 4s. 5½d. to 4s. 6d. per bushel, smutty was sold at 3s. 5d. to 3s. 9d. for inferior, and 3s. 10d. to 4s. for better samples. It is this necessity for having wheat almost absolutely bunt-free that has hitherto deterred experimenters from even making the attempt.

Experiments with Florence and Genoa to test their Bunt-resistance

This question of immunity to smut is a very important one, and experiments to test how far this immunity is hereditary or transmissible, and if it is maintained under different conditions of soil and climate, heat and moisture, were carefully planned. Mr Sutton willingly supplied seed-wheat of Florence and Genoa for the purpose, and a sufficient quantity of grain was mixed with bunt spores to allow of its being sown in such distinct districts of Victoria as Dookie Agricultural College, in the North, under the superintenddence of the principal, Mr. Pye; at Longerenong Agricultural College, in the West, under the charge of Mr. Pridham; and at Burnley Horticultural Gardens, near Melbourne, in the South, under my own personal supervision. The seed was all dusted equally with spores of *Tilletia levis*, derived from a common source, and it is important to note that the experiments were all on an equal footing as far as the amount and vitality of the bunt-spores are concerned. A bulk sample of wheat was mixed with the spores as follows:— Bunt-balls were taken direct from the wheat plant and then broken up by rolling them in paper. The spores were next well dusted and rubbed over the moistened grains, so that every grain looked as if it had been dressed with soot. The grain was sent out immediately afterwards for sowing.

At Dookie, the sowing took place on 17th June, and the seed-bed was a moist one. Superphosphate was applied at the rate of about 65 lbs. per acre. The rainfall for April was .23 inches; for May, 1.99 inches; and for June, 4.36 inches. The bunted grain sown in a moist seed-bed was particularly liable to infection. The mean temperatures for May and June were 11 and 7° C. respectively.

At Longerenong, the seed was sown on 1st June, and the seed-bed was in good condition and moist. The rainfall for April was .09 inches; for May, 3.22 inches; and for June, 2.55 inches. The mean temperatures for May and June were 10 and 7° C. respectively.

At Burnley, the plots were sown on 16th June, the soil being a sandy loam, and in a moist condition. The experimental ground was enclosed with bird-proof netting so that the results were not interfered with in any way. As this was the first season of the wheat experiments there, manure was supplied at the rate of per acre, 1 cwt. superphosphate, ½ cwt. sulphate of ammonia and ¼ cwt. sulphate of potash. The rainfall for April was .33 inches; for May, .87 inches; and for June. 3.94 inches. The mean temperatures for May and June were 11 and 8° C. respectively.

Since the weather conditions exercise an important influence on the germination of the spores, it may be noted generally for the first quarter of the year 1908, that the rainfall was scarcely 50 per cent. of the average amount and this was followed by one of the driest April months ever known. The breaking up of the drought occurred in May, and the rains in June were above the average, so that altogether, the conditions were favorable for the germination of the spores and the seed-wheat at the same time.

The results of the experiments have been carefully tabulated, and while they show that Florence may have as much as 12 per cent. of Stinking Smut, and Genoa, 22 per cent., yet on the whole, they are fairly resistant.

TABLE I.—RELATIVE SUSCEPTIBILITY TO STINKING SMUT OF FLORENCE AND GENOA.

Plot.	Variety.	Inoculation of Seed with—	Smutty.	Free.	Total.	Per cent. Smutty.
		I.—Burnley.				
5	Florence ..	*T. tritici*	2	82	84	2.38
6	Genoa ..	,, ...	7	71	78	9.
8	Florence ..	*T. levis*	10	69	79	12.65
9	Genoa ..	,, ...	5	78	83	6.02
12	Florence ..	,, ...	7	79	86	8.14
13	Genoa ..	,, ...	0	75	75	..
14	Florence ..	*T. tritici*	5	79	84	5.95
15	Genoa ..	,, ...	17	58	75	22.66
16	Florence ..	*T. levis*	41	818	859	4.77
17	Genoa ..	,, ...	41	774	815	5.03
	Florence ..	General Average	65	1,127	1,192	5.45
	Genoa ..	,, ,, ...	70	1,056	1,126	6.21
	Florence ..	*T. levis*—General Average ..	58	966	1,024	5.66
	Genoa ..	,, ,, ,, ..	46	927	973	4.72
		II.—Dookie.				
1	Florence ..	*T. levis*	1	84	85	1.17
9	Genoa ..	,, ...	1	74	75	1.3
2	Florence ..	*T. levis*, re-smutted ..	8	85	93	8.6
10	Genoa ..	,, ,, ..	5	76	81	6.17
3	Florence ..	*T. levis*	3	77	80	3.75
11	Genoa ..	,, ...	2	72	74	2.70
4	Florence ..	*T. levis*, re-smutted ..	3	83	86	3.48
12	Genoa ..	,, ,, ..	5	73	78	6.41
5	Florence ..	,, ,, ..	4	79	83	4.82
13	Genoa ..	,, ,, ..	14	72	86	16.28
	Florence ..	General Average	19	408	427	4.45
	Genoa ..	,, ,, ...	27	367	394	6.85
	Florence ..	*T. levis*—General Average ..	4	161	165	2.42
	Genoa ..	,, ,, ,, ..	3	146	149	2.
	Florence ..	*T. levis*, re-smutted ..	15	247	262	5.72
	Genoa ..	,, ,, ..	24	221	245	9.79
		III.—Longerenong.				
1	Florence ..	*T. levis*	45	443	488	9.22
2	Genoa ..	,, ...	95	560	655	14.50
3	Florence ..	,, ...	7	70	77	9.09
4	Genoa ..	,, ...	10	54	64	15.62
	Florence ..	General Average	52	513	565	9.20
	Genoa ..	,, ,, ...	105	614	719	14.60

I. *Burnley.*—There were seven plots of each variety sown, in two of them the ordinary seed was used as a check, while in the others the seed was thoroughly dusted with bunt-spores. Both *T. tritici* and *T. levis* were used for infection, but no conclusions as to their relative virulence could be drawn from the results of a single season's experiments. The general average for the whole of the plots was over 5 per cent. for Florence, and over 6 per cent. for Genoa. If the comparison is strictly confined to the plots in which *T. levis*

was used, as at Dookie and Longerenong, then Florence had 5.66 per cent. and Genoa 4.72 per cent. of Stinking Smut. In all cases the ordinary seed was sown as a check and the plots were invariably free from bunt.

II. *Dookie.*—There were also five plots of each variety sown here to test their susceptibility to bunt, and only *T. levis* was used. In order to make the test as severe as possible, some of the grain already dusted with spores was re-smutted in the following manner. One hundred smut-balls were powdered and then made into a soft paste by the addition of water. One hundred grains were placed in this paste, thus allowing one smut ball on an average for each grain, mixed thoroughly and allowed to soak over-night. By next morning the moisture had disappeared and the seed was sown the same day. Infection in the re-smutted grains was the most virulent, for while it yielded 5.72 and 9.79 per cent. of bunt respectively in Florence and Genoa, there was only 2.42 and 2 per cent respectively with the ordinary dusting of the grain. The general average for Florence was 4.45 per cent. and for Genoa, 6.85 per cent. The higher average for Genoa was largely owing to one plot in which the percentage was over 16, while in a plot alongside it was only a little over 6. This difference was so striking, that these two adjoining plots were again carefully examined with the same result. There was no evident cause for the unequal infection.

III. *Longerenong.*—There were only two plots of each sown, a large and a small one, together with the check plots, and the dusting of the seed was entirely with the spores of *T. levis*. The general average was much higher here than in the other two localities, being 9.20 per cent. for Florence, and 14.60 per cent. for Genoa. This may be due to the heavy rainfall in May.

It is clear, from the experiments, that Florence and Genoa no not possess the hereditary quality of bunt-resistance, and Sutton evidently suspected this, as he wrote to me as follows in May, 1908 :—"I have been referring to the results of our trials with these wheats while they were being fixed, and I find that in 1905, they were at Lambrigg fairly bunty, and this may indicate that they are not constitutionally resistant to bunt, but that they escape bunt through some peculiar characteristic of their growth immediately after germination." As elsewhere pointed out they are relatively rapid in their germination (see Frontispiece), and this may account for their escaping the bunt to a large extent. But in order to secure complete immunity and the hereditary quality of resistance, it will be necessary to breed from a variety which has shown itself to be free when exposed to the most severe infection for a series of seasons.

Experiments at Dookie Agricultural College.

Mr. Pye, principal of Dookie Agricultural College, had been working for some years in conjunction with Mr. Farrer in endeavouring to produce bunt-resisting wheats by selection after seed-infection. He is still continuing this work and the most promising line lies in breeding from crosses of the Durum variety, that resist the bunt. He found, for instance, that Medeah is not so liable to bunt as many others, and he is using this variety as a parent. The seed of the progeny is then dusted with bunt-spores and the seed from those plants which escape infection is sown next season, and so on until a strain is secured which will be bunt-resisting.

Not only have these experiments been carried on for a number of years, but they are conducted on a most comprehensive scale, as during the past season there were over 200 plots devoted to smuts alone. I have carefully examined them and find that it is necessary to determine the bunted plants when the growth is completed and all the ears are more or less mature. This

is owing to the fact that in many cases the secondary ears or later growths may develop the disease, while the more advanced ears of the same plants are free.

To show the methods adopted by Mr. Pye, some of the more important results will be given here and they will indicate clearly how far he has succeeded in producing a bunt-resisting wheat. Among the numerous varieties grown, there were several which promised to be more or less bunt-resisting, and these were used as parents for further crosses, but the only one found to be absolutely free this season, after the most thorough infection of the seed, was Medeah. Various selections and unfixed crosses are also being tested, and naturally those containing Medeah blood receive special attention.

Out of numerous selections from various crosses, only two were found to be clean after infection, apart from those containing Medeah. Ordinary seed was invariably sown alongside infected seed, and only in two instances was one plant found to be bunted.

In Table II. the number of selections from each cross is given with the proportion of bunted plants, and towards the end, all those crosses are recorded containing an admixture of Medeah blood.

TABLE II.—SELECTIONS FROM CROSSES, WITH PERCENTAGE OF BUNT.

Cross.	No. of Selections.	Percentage of Bunty Plants, varying from—
Queen's Jubilee .. .. Stanley	5	47 to 93
College Purple Straw .. .. .. Langshan × Stanley	3	40 „ 77
Langshan .. .. Stanley	2	56 „ 72
Burton .. .. Stanley	3	63 „ 75
Tripola .. .. John Brown	5	50 „ 83
Allorite .. .. Semi-Durum	3	11 „ 57
Langshan .. .. White Fife	1	28
Blue Heron .. .. Egyptian × Tardent's Blue	4	Free
Tripola .. .. Tardent's Blue	2	25 to 28
Tripola .. .. Tardent's Blue	1	Free
Tripola .. .. Tardent's Blue	3	6 „ 36
Tripola .. .. Tardent's Blue	3	6 „ 29
Missogen .. .. Medeah × White Fife	3	16 „ 50

TABLE II.—SELECTIONS FROM CROSSES, WITH PERCENTAGE OF BUNT—*continued.*

Cross.	No. of Selections.	Percentage of Bunty Plants, varying from—
Bobs × Medeah .. .. / Tripola	2	Free
Bobs × Medeah .. .. / Tripola	2	,,
Bobs × Medeah .. .. / Tripola	3	,,
Bobs .. .. / Medeah	3	One with 6 and two selections free
Bobs .. .. / Medeah	5	8 to 16
Bobs .. .. / Medeah	6	Free
Bobs .. .. / Medeah	3	17 to 30

Several of the crosses turned out bunt-free, particularly those into which Medeah enters. and it only remains to be seen after further trial if this is a hereditary quality. They will be tested in a similar fashion to Florence and Genoa.

The difficulty and uncertainty here lies in making sure that the bunt-free plants owe their resistance to constitutional characters, and not to the accident of the spores failing to germinate or the mycelium of the fungus inside the plant being unable to reach the ovary. I have had numerous examples in different seasons of ears being only partially smutted and the reasonable explanation is that from the nature of the season and the consequent growth, the mycelium had not sufficient vigour, or was not sufficiently nourished in the straw to produce spore-forming hyphae in every grain. The clean grains were taken from such partially-smutted ears and sown again after proper inoculation, when it was found that they were liable to infection, thus proving that there was nothing in the grain itself which caused it to escape. The question as to the hereditary character of the bunt-resistance can only be definitely settled by growing the seed from such bunt-resisting plants, for several seasons in succession, after being thoroughly dusted with spores and proving that immunity is or is not an inherent characteristic. Once an immune parent is obtained, then the desirable qualities to be associated with this immunity can be produced by further crossing. Attention has hitherto been so exclusively devoted to providing remedies for smut, that the attempt to produce smut-resisting plants is well worthy of being persevered with, and the experiments so far carried out are decidedly encouraging. There are thus, at least, two methods of procedure in seeking to obtain a variety of wheat immune to bunt, either to start from what is known as natural immunity, in which the plant from its very constitution inherits a certain amount of resistance, as in the case of Medeah, or by means of selection to arrive at a plant which has acquired this character, as in the supposed case of Florence. It was the idea of the late Mr. Farrer to inoculate the seed which produced the variable generation

of his new crosses with bunt spores, and then select bunt-free plants from the new generation, hoping thereby to secure an immune strain, or one at least less susceptible than the parents, But in either case, it has yet to be proved that immunity is absolute and complete, and that rich feeding or starvation, for instance, or the severity of the infection may not break down the power of resistance. Insufficient food is said to increase the susceptibility to infection in the human subject, but this does not seem to hold good for plants. Brooks[1] in his infection experiments with *Botrytis cinerea* used lettuce plants. as they are extremely susceptible to attack. He found that leaves just beginning to turn yellow were readily infected while normal green leaves were immune. When grown under different conditions of mineral starvation, they behaved similarly as regards infection to those grown under normal conditions. Just as Ward[2] found that, with *Puccinia dispersa*, the starvation of the host had no appreciable effect upon its ability or inability to cause infection, so here, the work on Botrytis confirms Ward's view that " Whatever may be the causes at work in the living cell which confer immunity or predisposition on the species of host-plant, or which confer virulence or impotence on the spore, they lie deeper than nutrition."

Since Stinking Smut of wheat is so easily and certainly prevented by means of pickling, there is not the same practical interest in producing a bunt-resistant wheat, as in producing a rust-resisting wheat for instance. But it must be remembered that there are other smuts, such as flag smut of wheat and loose smut of wheat and barley, which are not so amenable to treatment, and the methods by which a bunt-resisting wheat is obtained will also be applicable to the others.

Relative Virulence of Infection by Spores of T. levis and T. tritici,

It is well known in connexion with cereal rusts that a wheat may be immune or comparatively immune to one species of rust, and susceptible to another, so that it became necessary to determine if wheats reputed to be immune to bunt were equally so to both species. In the case of Florence and Genoa they were liable to infection by both *T. levis* and *T. tritici*, but in varying degrees. Experiments were carried out specially with two other wheats, viz., Dexter and Federation, to see how far the two species of bunt differed in their capacity for infecting them. Sound seed was sown in each case along with the infected, and the sound seed invariably yielded healthy plants. The results are given in the following Table and compared with those obtained from Florence and Genoa collectively :—

Table III.—Relative Amount of Infection by T. levis and T. tritici respectively.

Infected with—	Dexter.			Federation.		
	Bunted.	Clean.	Per cent. Bunted.	Bunted.	Clean.	Per cent. Bunted.
T. levis	43	37	53.75	55	21	72.36
T. tritici	36	45	44.44	43	45	48.86
Mixed spores, but mostly *T. levis*	..	..	..	547	365	59.97
	Florence.			Genoa.		
T. levis	166	2,153	7.71	259	2,301	10.11
T. tritici	7	161	4.16	24	129	15.6

It will be seen from the above that *T. levis* is generally the most virulent; but in the case of Genoa it was the reverse, *T. tritici* being considerably more so.

It has been pointed out by Harwood[1] that there is an evident difference between the wheat attacked by *T. tritici* and *T. levis*. With the former the stalks are as tall as those with healthy grain, while with the latter they are shorter, and this difference is so striking that in some parts of Michigan they are spoken of respectively as "high" smut and "low" smut. This would seem to indicate that the one smut interferes with the growth of the wheat plant much more than the other, but in our plots there was no perceptible difference between the two.

Rapidity of Germination and Smut Liability.

It is well known that wheats vary considerably in their susceptibility towards stinking smut, and that while some varieties are very liable to it, such as Allora Spring, others are very resistant, such as Minnesota Blue Stem and Medeah. Dr. Appel[1] of Berlin observed that a square-head wheat originally grown in Ohio was susceptible in a very slight degree, and that it germinated so quickly that it very soon passed the stage when it was capable of infection by the germinating spores of the smut. It is believed that this rapid germination is associated with a lessened liability to smut, as other varieties with similar properties germinated quickly, but we have yet to ascertain whether this is a principle of general application as regards the wheats grown in Australia. Kirchner[1] has investigated a large number of spring and winter varieties to see if any relation exists between their susceptibility to bunt and their germinative energy. He did not find that a low germinative energy was associated with susceptibility, nor that a high germinative energy was an unfailing character for determining bunt resistance. But Hiltner[1], who found that rapid germination is characteristic of wheats that withstand the smut, points out, with reference to Kirchner's results, that a good deal depends on the mode in which the germination is conducted. The author, with his specially constructed germinating apparatus, found that oats from one district germinated 90 per cent. in five days, and from another district in the same time 35 per cent.; but when tested in the usual way, between moist blotting paper, there was no distinction shown in the germinative energy of the two.

Any tests made in connexion with the relative rapidity of germination are worthy of being recorded, and the following refers to four varieties. I received a sample of Ohio wheat and germinated it along with Florence and Genoa, which are comparatively resistant to bunt, as well as Warden, which has proved itself to be very susceptible. The seed was sown at an even depth in shallow pans in a sandy loam, and well watered. As the weather was very warm at the time, germination was rapid, and in four days two seedlings of Ohio were above ground and one of Genoa. In six days the totals were—Ohio 6, Genoa 4, Florence 16, Warden 14; and in eight days—Ohio 20, Genoa 16, Florence 18, Warden 18. The photographs in the frontispiece show well the relative rapidity of germination and strength of the seedlings of each variety, and it will be noted that the Ohio was much the most vigorous, the Genoa and Florence being about equal, and the Warden much slower and weaker. These differences in vigour tended to disappear with age, till on the fifteenth day there was no perceptible difference between the Ohio, Florence, and Genoa, though the Warden was scarcely so forward (Frontispiece).

Escape of Infection by individual Plants.—It is quite a common observation that when the individual plants of a variety of wheat are all dusted equally

with bunt spores derived from a common source, in the same way at the same time and sown on the same day in similar soil alongside each other, they are not all equally infected. Even in the most favorable cases there are generally a number which escape, and it requires to be explained how some are smutty and others not. There are various reasons which may be assigned and there are a number of conditions which must obtain at the same time for successful infection. It need not be assumed that the failure is due to the non-germination of some of the spores, for the germ-tube may penetrate into the host-plant and yet not necessarily produce infection.

In the first place, the host-plant must be at the right stage of development when the spore or conidium has put forth its germ-tube, and this period in the young seedling does not last very long. Further, when the germ-tube has penetrated into the seedling, it must reach the growing point, otherwise it would not continue to keep up with the growth of the host-plant and finally produce smutty ears. Now, the slower this stage of growth is the more likely it is that the germ-tube will reach its destination in time, whereas the more rapid the growth the less likely it is to reach the growing point of the young seedling before it begins to elongate. It is well known that individual grains vary in the rapidity of their germination, and this might be so hastened that the penetrated germ-tube would fail to reach the growing point. This suggests another reason for some of the plants escaping infection. Some varieties are very slightly susceptible to infection by bunt, and only some of the plants would under these circumstances become smutty. This applies particularly to Florence and Genoa, which are only slightly susceptible, and in the case of Medeah it was the only one dusted with spores which escaped infection entirely during 1908. In fact, the whole question of Parasitism and Immunity or Susceptibility and Insusceptibility to disease, seems to be bound up with the presence or absence of certain chemical substances in the host-plant. Miyoshi[1], of Japan, was the first to show that the germ-tube of a fungus will only enter the tissue of a living plant and develop there when the special substances which attract it are present. This sensitiveness to certain chemical substances possessed by the fungi is known as Chemotaxis, or Chemotropism, and the substance which exercises this attractive influence is spoken of as a positively chemotactic substance. Miyoshi demonstrated that the hyphæ of *Penicillium glaucum* for instance, pierced the epidermis of living leaves when previously hypodermically injected with a chemotactic substance such as sugar, and Massee[3] proved that certain cucumber plants were immune to a disease to which they were normally subject, owing to the absence of the special substance which attracted the parasite. The quantity, as well as the quality, of the dissolved substances and their unequal distribution influence the result; and some substances are not only negatively chemotactic, but they are positively injurious, and repel the entry of the parasite into the tissues of the plant. It is easy to understand that in the early stages of the seedling there will be a variety of substances dissolved in the cells, and these may vary considerably in the neighbourhood of the growing point. Sugar is the substance which is the great source of attraction to the germ-tubes of fungi, and this will vary considerably in amount, according to the nature of the growth, and may even be neutralized in its action by the presence of other substances.

For individuals of the same variety we must assume a slightly hastened or retarded development in the seedling stage, and a quicker or slower growth afterwards, in order to account for the unequal infection; but this will necessarily be associated with a variation in the chemical composition of the substances in solution in the plant.

This unequal infection is the crux of the whole position, and if we could account for it satisfactorily it would help us to understand the conditions under which infection occurs. At the present time the germ theory of infectious disease in the human subject is on the eve of being considerably modified, and this has a direct bearing on infection in plants. The smut fungus produces its spores, and these, like the tubercle bacilli for instance, give rise to certain symptoms in the host, which only occur in association with this particular kind of organism. Further, the spores, like the pathogenic or disease-producing germs, have been isolated from the plant-body, cultivated on artificial nutritive media, and then studied in the laboratory. But it has been found that organisms which cannot be distinguished from pathogenic germs exist in the tissues of persons who are apparently in perfect health, and such persons have been designated as "disease-carriers." Here is a case where the organism, supposed to be the definite causal agent, is present without the symptoms, and the idea is gaining ground that the so-called pathogenic germs are ordinarily harmless, but they require certain conditions to develop their virulent properties. Just as the infection thread from the germ of the smut can penetrate the plant but cannot produce infection in the presence of substances known as chemotactic, so in the human subject something is required to co-operate with or oppose the germs, before they can be expected to show pathogenicity or the reverse. In the plant, sugar is the great attraction for the parasite, and since sugar is usually associated with ferments, it may be that in both plant and animal something of the nature of a ferment must be present to excite the germs to activity, and so the "Ferment" theory of infectious disease may yet explain why under seemingly similar conditions the germ is pathogenic or disease-producing in the one case but not in the other.

CHAPTER IX.

Relations between Host and Parasite in Smut Diseases.

The smut fungi, which are dependent upon certain host-plants for their existence, very frequently convert the seed into a black mass of spores, and when this is done in a wholesale manner, the host-plant is unable to reproduce itself. I had an instance of this in the case of Brome smut in the early part of 1907, when a paddock sown with prairie grass (*Bromus unioloides*), in which the seed supplied was smutted, showed not a single plant free from the disease. The seed of the host-plant was entirely destroyed, and if this were to happen over a large area, in the case of an annual such as wheat, the fungus itself would run the risk of becoming extinct from the failure of its food supplies. The law of self-preservation comes into play here, and the total extinction of the host-plant may be guarded against by some of the grains becoming more resistant to the entrance of the parasite on germination than others. The less resistant would succumb, while the more resistant would survive, and by a process of selection it might eventually come to pass that a race of plants would be produced immune to the parasite. We have a parallel case in the human race in connexion with pulmonary consumption. As Sternberg[1] points out, there are certain races which may be specially liable to infection by the tubercle bacillus, while there are others such as Russian and Polish Jews, which enjoy comparative immunity, as shown by vital statistics. But the same principle applies generally to infectious diseases, and the above-mentioned author, in his recent work on "Infection and Immunity," clearly expresses it as follows:—"In general, it may be said that when an infectious disease is first introduced among primitive races, who, by reason of their isolation, have been previously exempt from it, it is apt to be exceptionally fatal. This is, no doubt, due to the fact that there has been no opportunity for the operation of the laws of natural selection, by survival of the fittest. But under the operation of these laws, in process of time, a certain degree of race immunity is likely to be established."

In drawing analogies from human diseases it may not be out of place to remark that the eminent surgeon, the late Sir James Paget, considered that the study of plant diseases might be very helpful to human pathologists. In an address on "Elemental Pathology" delivered before the British Medical Association, at Cambridge, in 1880, he pointed out that many of the morbid processes occurring in plants are quite comparable with those occurring in animals, such as hypertrophy or excess of nutrition, atrophy or defect of nutrition, repair of injuries and even inflammation in plants, which has since been elaborated by Dr. Ransom in his work on "The Inflammation idea in General Pathology." It is in the field of parasitism, however, that the likeness is most striking, and which Paget considered the most worthy of study, for he says:—"But of all morbid processes in plants, none, I think, are so suggestive as are those produced by parasites, whether vegetable or animal." I can foresee a great advantage in thus regarding plant diseases as part of the general phenomena of disease, not merely as aids to human pathology, but in turning human pathology to account in the investigation of diseases of plants. It has been too much the custom hitherto to consider plant pathology as a thing apart, as dealing with a class of disease which had nothing in common with the great discoveries in the domain of bacteriology, for instance, From this point of view great possibilities are opened up, and investigations are suggested which might otherwise be overlooked. The questions of

immunity and parasitism when studied as they affect the plant, with the wider outlook derived from considering their bearing upon and connexion with men and animals, are more likely to be fruitful in results and less liable to be misunderstood. Bacteria, in their relation to plants, and plant sanitation, are now receiving attention, and this is but the beginning of a new era in the mode of regarding plants as affected by disease.

There is a sort of reciprocal action going on between host and parasite. On the one hand, the more perfect the fungus becomes as a parasite, the more deadly will be its effects on the host-plant, and, on the other hand, the more resistant the host-plant becomes, the less chance will the parasite have of surviving, unless it changes its host. But there is a common ground of agreement in the fact that, while it is to the interest of the parasite that the host should not become extinct, it is also naturally to the interest of the host that it should survive, and the final result is that the general tendency is in favour of the preservation of the host. The question is not so much Which is to conquer in the struggle for existence? but if one organism is favoured at the expense of another, how is that other to maintain its ground notwithstanding the struggle.

There are various ways in which this may be accomplished, and a few may be recorded here.

1. The most permanent means would be the production or development of immunity in the plant itself, so that, instead of being predisposed to the disease, it would have hereditary tendencies in an opposite direction. This immunity may be more or less complete, and it is strongly developed in the Durum varieties of wheat.

2. The germination of the seed may be so rapid that the young seedling will outstrip the germinating spore of the parasite, and thus be too far advanced for successful infection to take place. This property of rapid germination is associated with various varieties of wheat, and it has been shown experimentally that an Ohio variety of wheat, also Florence and Genoa, which are highly bunt-resistant, are relatively rapid in their germination, while a well known bunt-liable variety such as Warden is comparatively slow.

3. There may be a form of symbiosis established between parasite and host which will enable both to thrive in partnership. This is apparently the case with the seed fungus of *Lolium temulentum* or Darnel, which has been investigated by Freeman, [1,2,3] and is now considered to be a smut.

In some of the smuts, such as the loose smut of oats, there is a profuse development of spores, and consequently a relatively large destruction of the host-plant. In loose smut of wheat, where infection takes place through the flower, the parasite passes the first stage of its existence in the seed. If the seed germinates and the conditions are favorable, there will be a production of spores in the plant produced, but it is conceivable that spores may not be formed, and then this would lead up to the case of the smut in Lolium. There the mycelium of the fungus occurs in the seed, and a mutual understanding is set up between the smut and its host-plant by the production of spores being kept in abeyance. "The Lolium fungus symbiosis is therefore apparently to be explained as a development from a smut parasitism of the loose smut of wheat type, in which the spore formation is entirely lost or of very rare occurrence, and in which a compensating mycelial infection of the host-plant embryo has been substituted for it." In short the parasite here has to be contented with a purely vegetative existence, and seems to exert a beneficial influence on the host, for cultures showed that mycelium infected seeds generally produced more vigorous plants and a greater number of seeds than the uninfected. It is known that some Darnel seeds

are free from the fungus, although this is only discernible by the microscope, and that they produce plants likewise free; but the poisonous property, due to the alkaloid Temulin, is only developed when the fungus is present. This has been shown by Hannig,[1] and the production of this toxin by the fungus may prevent its complete development just as the production of alcohol will ultimately overpower the yeast. This raises the further question whether immunity may not be due to the production of toxins and anti-toxins by both the parasite and its host, which neutralize the effects of the parasite in the host or may actually destroy it.

The parasite as well as its host feeds and excretes, and the excreta are probably toxic, so that when the nature of the toxins and anti-toxins in the plant body is better understood and when they have been isolated and studied, then some light will be thrown on the cause of immunity itself.

Potter[1] has shown how parasitic diseases in plants may be checked by taking advantage of this property of the waste products of metabolism, when allowed to accumulate beyond a certain stage, checking the growth and finally proving fatal to the parasite. He prepared a toxic solution in pure cultures of the parasite which was not only fatal to it, but as might have been expected, exercised also an injurious influence on the healthy cells of the host. This influence, however, only extended to a limited area, and the wound soon healed over. By this means he was able to arrest the decay caused by a *Bacterium* and a *Penicillium*, so that the principle is probably applicable to parasites in general.

4. This absence of spore formation in the seed may be due to hereditary tendencies, as in the Lolium, or it may be brought about by external agencies which affect the growth, and are intermittent in their character. Thus the host-plant may not have every ear attacked, so that in the case of "tillering" of wheat, some ears of the same individual plant may be completely free from the parasite. Or only some of the grains in an ear of wheat may be attacked, as happened particularly during season 1907, when there was only a short growth of straw, but the weather at blooming time favoured the production of large and vigorous ears.

If we take the concrete instance of bunt in wheat it will be seen how host-plant and parasite get along together. As soon as the smut has infected the seedling and the germinal hyphæ have reached the growing tissue, the curious result is that they both grow together, and there is an inducement for the host-plant to provide for both, as it is constantly stimulated thereto by the hyphæ growing between the cells. This concurrent growth of host and parasite goes along smoothly and without any external sign of disorder until the grain begins to be formed. Then there is a struggle for existence as to whether the host or the parasite is to be the winner in life's race, for from the very nature of the case, unless the parasite produces its spores it is likely to succumb, and, on the other hand, if the embryo is not formed, there will be no future host-plant. It is a struggle in which it is apparently war to the death, and the more successful the parasite is the more injurious it is to the host. But what decides whether the host or parasite will win? Well, there may be a temporary truce when some ears, or it may be only some grains in the ear, escape destruction by the parasite. But, in the long run, among the combination of causes which favour the preservation of one or other organism, it will be found that a compromise has been arrived at, and the tendency to become immune is the important factor in enabling both the smut and its victim to survive in the struggle. I have only noticed the more evident factors in the struggle; but it is really between the tissues of the host-plant on the one hand and the germinal hyphæ and mycelium of the parasite on the other, and whatever external influences

affect the one or the other injuriously or favorably will have a bearing on the result. Thus, if the autumn is wet when the seed is sown nearly all the seeds with spores attached will become infected, because the tissues under such conditions remain longer soft and succulent. There are also limitations imposed upon the germination of the spores, for they are not always capable of putting forth their germinal tube at any given time even when moisture is supplied.

It is a general characteristic of smut fungi that they confine themselves to particular hosts. This denotes a high degree of specialization in thus exercising a selective power for their food, for there are other parasites which are omnivorous in their tastes and show little or no preference in their selection of hosts.

Some of them such as the American corn smut utilize any young and tender portion of the plant, be it leaf or stem or kernel of the cob, and whenever it is attacked do not at once proceed to use it up in its immature state. The fungus stimulates the young and growing part to further growth, and when it has multiplied excessively so as to form gall-like swellings, the food stored up is rapidly appropriated and the spores are produced from a well nourished and vigorously growing mycelium. Not only do they select a host but in many cases they are only capable of infecting a particular stage of that host, such as the seedling stage or the flowering stage. When the young seedling is infected, the parasite puts itself in touch with the growing tissue and shares in all the growth and vigour of the plant until the critical time arrives, when all the nutrient material prepared for the young embryo is used up in the formation of smut spores.

But the perfection of specialization is reached in the Carnation Smut fungus, where the anthers of the flower are alone chosen for the production of the spores. The parasite enters the plant through the young shoots as shown by Hecke, and reaches the flower just before it is completely formed. There it confines itself to the young stamens, using the anthers for the production of spores and leaving the rest of the flower quite normal. It is the doctrine of substitution carried to its utmost limits, for not only have the spores replaced the pollen-grains, but they are carried by the fertilizing insects to other flowers, and thus their distribution is assured as they are likely to be deposited on the fruit which is being formed. This is an instance where the fungus has selected the most favorable spot for the production of spores, and timed it so that they are carried to their destination as if they were the flower's own pollen. There are degrees of proficiency in the parasite, just as there are powers of resistance in the host, and this is the highest attainable in the mode of infecting the most suitable part at the most favorable time.

In considering the relations of the parasite to its host, we must take into account all the phases of its life and distinguish between those which are intimately bound up with the life of the individual plant and others which are passed outside of it. The mycelium of the fungus, for instance, ramifies among the tissues and directly preys upon them, but there are portions of the hyphæ detached at the surface for purposes of rapid propagation and known as conidia, which are used to infect fresh plants. These conidia are known to vary in their infective power, not only as we have seen, according to the condition of the host, but dependent upon the nourishment they receive and their age as well, or the generation to which they belong. If the mycelium which produces them is well nourished, then as parts of the whole, they share the increased vigour for a time, but with increasing age and the continued absence of a host-plant they lose their capacity for infection. Brefeld[1] has shewn that these conidia can germinate in artificial nutritive solutions and go on producing generation after generation of their kind. He cultivated one form through more than one hundred successive generations in the course of

a year, but towards the end their germinating power began to fail and at last failed completely. "Smut germs which have lived too long and too exclusively outside of the host-plant and multiplied in the form of yeast conidia lose their infective power conjointly with the ability to throw out germ-tubes."

It has also to be noted that the climatic conditions which favour the parasite are not always those which are most conducive to the well-being of the host, especially when it is being attacked from the outside. The dull, damp, cold weather which makes its tissues tender and renders its functions less active are just those conditions which favour the entrance of the fungus, and if the latter once reaches the growing-point, it is as certain to succeed as the plant itself. Brefeld has shown this beautifully by demonstrating that if the conidia are forced into the bud by means of a syringe, so that they can germinate in contact with the young and growing cells, infection can always be assured.

There is, generally speaking, a double set of factors involved in each case of parasitism, the internal disposition or constitution of both host and parasite and the external influences or environment affecting each. It is in the mutual play and interaction of these factors that all the varied and varying effects are produced, and it can therefore be readily understood that no single cause or set of factors will explain any case of parasitism, but that the life-history of both host and parasite must be considered and all the agencies which affect one or other favorably or unfavorably must be taken into account. The study of the parasitic diseases of plants, or the mutual relations of host and parasite, thus becomes a very complicated problem, and the recognition of the factors acting in concert or successively which bring about the changes giving rise to disease, is the only way to arrive at its true nature. While it is true that no single factor is entirely responsible for a disease, yet it is customary to classify diseases according to their chief causes. John Stuart Mill says that "in practice, that particular condition is usually styled the cause, whose share in the matter is superficially the most conspicuous." In this sense the weather might be said to be the "cause" of some parasitic plant diseases, as they are conspicuously associated with particular weather conditions. But among the various factors concerned, that one without which none of the others would be effective in producing the particular symptoms, may be more truly termed the cause. Hence when the presence of a fungus, such as the smut-fungus, is absolutely essential to the production of a well-marked disease, it is the direct cause of it, even although such a co-operative factor or contributing cause as the weather is necessary.

CHAPTER X.

Indigenous and Introduced Species.

It is not always easy to determine what parasites are native and which have been introduced, because although the introduced plant is liable to carry with it the spores of some of the fungi which infest it in its native country on the seed, or it may be only the hibernating mycelium inside the seed, yet this is not invariably the case. While the potato has introduced into New Zealand and Australia the well-known potato disease *Phytophthora infestans*, the orange and the lemon in New South Wales are badly affected with a disease caused by *Phoma citricarpa*, a fungus which is unknown elsewhere, either in Italy or California, and which has probably been derived from the native Citrus trees. It will be safe, however, unless we have evidence to the contrary, to regard as introduced those parasites which are found on introduced plants.

The term *alien* is usually applied to those species which, although now growing spontaneously, have been introduced through human agency. Such alien plants are, therefore, often called introduced plants, although we may have no definite information as to how they were brought here. In the case of cultivated plants, such as cereals and some grasses, there is historic evidence as to their introduction, but beyond that there is very little certainty. A species, therefore, which is found wild amid natural surroundings may be regarded as indigenous, while those found amid artificial surroundings or as escapes from cultivation, may be considered introduced.

The introduced plants with smuts are confined almost exclusively to the cereals, such as wheat and oats, barley and maize, and to a few grasses such as rye-grass and *Poa*. From the principles laid down, the following may be regarded as having been introduced :—

1. *Ustilago avenæ* (Pers.) Jens., on *Avena sativa*, or Oats.
2. *U. hordei* (Pers.) Kell. and Sw., on *Hordeum vulgare*, or Barley.
3. *U. nuda* (Jens.) Kell. and Sw., on *Hordeum vulgare*.
4. *U. tritici* (Pers.) Jens., on *Triticum vulgare*, or Wheat.
5. *Cintractia sorghi-vulgaris* (Tul.) Clint., on *Andropogon sorghum*.
6. *Sorosporium reilianum* (Kuehn) McAlp., on *Zea Mays*, or Maize.
7. *Tilletia levis* (Kuehn), on *Triticum vulgare*.
8. *T. tritici* (Bjerk.) Wint., on *Triticum vulgare*.
9. *T. striaeformis* (Westd.) Oud., on *Lolium perenne*, and *Poa annua*.
10. *Urocystis tritici*, Koern., on *Triticum vulgare*.

There is no difficulty in accounting for the introduction of the above smuts as the spores would be associated with the seeds, or the hibernating mycelium would be inside the seed, as in the case of loose smut of wheat and barley, and both spores and mycelium retain their vitality sufficiently long to allow them to be transported long distances.

The only case calling for special remark is that of flag smut on wheat. It is generally assumed to be the same species as that found on Rye in the Old World, but since the spores from wheat will not infect rye, nor the spores from rye infect wheat, it must be biologically distinct, and as a biological species it may be called *Urocystis tritici*, Koern. The same form has also been found on wheat in India and Japan, but how this biological species originated it is impossible to say.

The total number of species at present recorded for Australia is sixty-eight. They are grouped under ten genera, and no new genera have been discovered as in the case of Uromycladium among the rusts. There are two gall-forming species, however, which are interesting, not merely from their producing galls, but on account of their distribution. *Melanopsichium Austro-Americanum* occurring on species of Polygonum, was first recorded from South America, then it was found in the United States, and now it has been met with near Brisbane, in Queensland. The Queensland specimen was first determined by Mr. Broome as *Ustilago emodensis* Berk., but an examination of the original type of this at Kew showed it to be quite distinct. *Cintractia crus-galli* occurring on the common Barn-yard grass, is widely distributed in the United States, but has only been found elsewhere near Sydney. A number of affected plants were observed by Mr. Hattrick growing in sandy soil, and they attracted his attention by the large galls formed on the stems. Both these gall-forming plants are adapted for moist situations.

Ustilago cynodontis may also be regarded as indigenous, since the host-plant —*Cynodon dactylon*—is a native. It occurs in Europe, Northern Africa, and India, to which Australia has now to be added.

The distribution of the species in the different States is very unequal. In Victoria there are about double the number recorded for any other single State, and this only shows how imperfectly known the smuts are. They do not generally attract the notice of collectors, and in some cases they are inconspicuous and not easily recognised when the spores are enclosed in the fruit. In West Australia only those species are known which attack cultivated crops, and those occurring on the native flora have yet to be discovered.

The following list shows the distribution of the species :—

——	No. of Species.	Victoria.	New South Wales.	Queensland.	South Australia.	West Australia.	Tasmania.
Ustilago	18	12	7	8	10	4	9
Melanopsichium ..	1	..	..	1	..	..	..
Cintractia ..	11	7	1	4	2	..	1
Sorosporium ..	13	6	8	6	1	..	2
Thecaphora ..	2	1	1	..	..	..	2
Tolyposporium ..	7	4	2	2	..	1	3
Tilletia	6	5	2	2	3	2	2
Entyloma ..	2	1	..	1	..	..	..
Urocystis ..	7	7	1	1	1	..	..
Doassansia ..	1	1	..	..	..	..	..
Totals ..	68	44	22	25	17	7	19

The smuts have not received the attention of collectors like the rusts, and only nineteen new species have been added to the following genera :—Ustilago (2), Cintractia (3), Sorosporium (6), Thecaphora (1), Tolyposporium (4), Tilletia (1) and Urocystis (2).

II.

LIFE HISTORIES AND TREATMENT OF CEREAL SMUTS.

CHAPTER XI.

Life Histories of the Cereal Smuts.—Introductory.

Since the smuts are all parasitic in their nature and cause disease in quite a number of our economic plants, investigations have been directed, not only towards gaining a complete knowledge of their history, but also a practical means of preventing their ravages. In order to control their course and counteract their influence it is essential to have a knowledge of their life history and mode of attack, how they gain a footing in the plant, how they reach the stage when spores are produced, and how these spores behave until the plant is again infected.

The first step in working out their life history was taken when Prevost[1], at the beginning of the nineteenth century, established the fact that the spores when placed in water germinated, and since then various investigators, including Tulasne, Kuehn, De Bary, Fischer von Waldheim, and Brefeld, have advanced our knowledge until at the present time Brefeld has followed their history from spore to spore, and given us a complete account of some of the more important smuts. Only the cereal smuts will be dealt with here, on account of their economic importance, including those which occur in wheat, oats, barley, and maize. In our wheat fields there are three which do considerable damage, and require to be carefully attended to with the extension of the wheat-growing area, viz., stinking smut or bunt (*Tilletia tritici* and *T. levis*), loose smut (*Ustilago tritici*), and flag smut (*Urocystis tritici*). In oats there is only the loose smut (*Ustilago avenae*), and in barley there are the two species known respectively as naked and covered smut. In the one case the smut is enclosed in a membrane which soon breaks, and the spores are scattered as in loose smut (*Ustilago nuda*), while in the other the smut is enclosed in the unbroken walls of the ovary, and generally remains solid after maturity (*Ustilago hordei*). In maize there is only one smut known here, which is commonly called head smut, because it attacks the entire head (*Sorosporium reilianum*), but this has so frequently been confounded with the corn smut so common in America that an account of the latter is also given. A great deal still remains to be done before anything like a complete account can be given of the life histories of the various Australian smuts; still a beginning has been made, and when the gaps are known it may lead to their being filled up all the sooner.

In order to give a connected view of the cereal smuts and their different peculiarities, I have arranged them in tabular form, and one of the most striking features is that they naturally resolve themselves into two groups, according to their mode of infection—flower infection and seedling infection. Among the flower infection forms there are only two, the loose smut of wheat and the naked smut of barley. Both give rise directly to a mycelium on germination without the formation of conidia, and the spores are scattered naturally at the flowering season.

Table of Cereal Smuts.

Cereal.	Kind of Smut.	Scientific Name.	Nature of Spores.	Germination of Spores.	Dispersion of Spores.	Mode of Infection.	Preventive Measures.
Wheat	Stinking smut	Tilletia tritici and Tilletia levis	Spherical, and with net-like marking; irregularly spherical, smooth	With promycelium and crown of conidia	Threshing time	Seedling ..	Steeping of seed
	Loose smut ..	Ustilago tritici	Spherical and finely warted	Directly forming mycelium	Flowering time	Flower infection	Hot water treatment of seed
	Flag smut ..	Urocystis tritici	In balls, with sterile peripheral cells	With promycelium and crown of conidia	Before and up to flowering time	Seedling and young shoots	Rotation of crops, as the spores are in the soil
Oats	Loose smut ..	Ustilago avenae	Spherical and finely warted	With promycelium and conidia	Flowering time	Seedling ..	Steeping of seed
Barley	Naked smut ..	Ustilago nuda	Spherical and finely warted	Directly forming mycelium	Flowering time	Flower infection	Hot water treatment of seed
	Covered smut	Ustilago hordei	Irregular to spherical, and smooth	With promycelium and conidia	Threshing time	Seedling ..	Steeping of seed
Maize	Head smut ..	Sorosporium reilianum	Spherical and densely warted	With promycelium and conidia	Flowering time	? ..	Use of healthy seed
	Corn smut ..	Ustilago zeae ..	Spherical and bluntly echinulate	With promycelium and conidia	At all times during growth of plant	All young and growing parts	No known preventive

With the increase in our knowledge of the life histories of the cereal smuts, it has been found necessary to split up some of the older collective species, both on account of their morphological and physiological characters, into several new species. *Ustilago segetum* (Bull.) Dittm. and *U. carbo* Tul. were originally used to include several of the species occurring principally on wheat, oats, and barley, and these names have now been discarded and replaced by others.

At first the old species *U. segetum* was split up by Jensen[1], in 1888, into the following four races :—*U. segetum*, var. *tritici*; *U. segetum*, var. *avenae*; *U. segetum*, var. *hordei*, form *nuda*; *U. segetum*, var. *hordei*, form *tecta*. And he showed, at the same time, that the smuts occurring on wheat, oats, and barley were only able to infect the particular cereal on which they grew.

Then in the same year Brefeld found that the loose smut of wheat and barley did not produce conidia on germination, and that their spores were incapable of infecting oats. On these grounds he constituted a species *U. hordei*, Bref., for the forms occurring on wheat and barley. In 1890, Rostrup[1] named the form *tecta*, determined by Jensen, *U. jensenii*, Rostr., because the spores produce a promycelium with conidia.

And, finally, in the same year Kellerman and Swingle[3] raised Jensen's two forms on barley to the dignity of species, and named them respectively *U. nuda* (Jens.), Kell. and Sw., and *U. hordei* (Pers.), Kell. and Sw., so that Brefeld's *U. hordei* was split up into the three species now retained—*U. tritici*, *U. nuda*, and *U. hordei*.

The names that will be adopted in this work are the following :—

U. avenae (Pers.) Jens. (1889)—forming conidia on germination.
U. hordei (Pers.) Kell. and Sw. (1890)=*U. jensenii*, Rostr.—forming conidia on germination.
U. nuda (Jens.) Kell. and Sw. (1890)—forming no conidia on germination.
U. tritici (Pers.) Jens. (1890)=*U. hordei*, Bref. (in part)—forming no conidia on germination.

CHAPTER XII.

Stinking Smut or Bunt in Wheat.

(*Tilletia tritici* (Bjerk.) Wint.; *T. levis*, Kuehn.)

Perhaps there is no smut better known to the Australian farmer than this one, since although it remains enclosed until harvested, it gives forth a disagreeable odour like stinking fish, especially when crushed, and one cannot fail to detect its presence. The spores do not escape as a powder, but are enclosed in the ovaries and glumes, and although at first somewhat greasy, they soon become dry and hard; and the mass of spores in an ovary is known as a bunt-ball, hence it is frequently spoken of as ball smut, and sometimes, on account of its hardness, as stone smut. Since the spores do not burst through, but are enveloped by the outer coats of the ovaries, it requires the practised eye to detect the disease at first (Plate II.). The ears are rigid, and of a somewhat darker green colour than the normal, the spikes are rather smaller, and a little further apart, and stand out more from the axis of the inflorescence, and the grains themselves in the early stages are of a deep dark unhealthy green, and the upper straw is of a peculiar bluish-green colour. The growth is arrested earlier than in healthy plants, so that there is premature ripening, and the leaves indicate the diseased condition by their yellow colour. There is the disagreeable smell where the disease is plentiful, which is due to trimethylamin, a decomposition product of the nitrogenous constituents of the parasite.

There are two species of smuts responsible for this disease, the one with smooth and the other with netted spores, but as both sometimes occur in the same ear of wheat and generally agree in their life history, they will be treated here as practically the same.

Germination.

This was one of the first species in which the germination of the spores of smuts was observed. Prevost[1], in 1807, germinated them in water, and figured not only the promycelium, but also the primary and secondary conidia. These observations were confirmed by a number of later observers, and Tulasne[1], in 1854, investigated the subject more fully. In 1858, Kuehn[1] fully described the process, and then, in 1883, Brefeld[1] added to our knowledge by showing how the spores behaved in a nutritive solution.

The spore germinates in water or after being kept damp for two or three days. The spores germinate freely under the following conditions:—Place them on damp blotting paper on a plate under a bell jar, keeping them moist for a few days, and the fine white mould which soon appears constitutes the promycelia and the numerous sickle-shaped conidia of the germinating spores. Or take a plate of plaster of Paris sprinkled with spores and place it in water under a bell jar. In about three days there is a copious production of conidia. The outer membrane of the spore splits, and a stout promycelium of varying length is produced, which elongates at the apex. When this reaches the air a tuft of thread-like branches is formed at the apex, and these constitute the conidia. After all the protoplasm has passed into them from the promycelium, they are cut off by a cross partition or septum, and if the promycelium happens to be very long, then numerous septa are formed from below upwards. The length of the promycelium will vary according to th distance to be traversed before it reaches the air, since conidia are only forme

G. H. Robinson, Phot.

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in the air and not in fluid. If germination takes place in damp air then the promycelium is short, but if in a dense layer of water then it is long. The contents of the spore pass into the tube, and then the contents of the tube collect in the growing apex, and if this grows further the tube becomes divided regularly by transverse septa. Lateral branches may also be formed which grow in a similar fashion.

The mature conidia are filiform bodies arising from fine tubercles at the apex of the promycelium, curved in various ways and varying in number from four to twelve or more. They usually become united in pairs by the outgrowth of a narrow tube passing from the one and fusing with the other, giving the appearance of the letter H. After this fusion germination occurs by the production of a slender filament bearing a sickle-shaped secondary conidium at its apex, into which the contents of the united spores have migrated. According to Kuehn[3] both the primary and secondary conidia when placed in a damp atmosphere can give rise to a germ-tube which is capable of infecting the wheat plant.

The primary conidia may become detached before germinating, and then fusion between them is not so likely, but when it occurs the connecting bridge is wider. Brefeld found that the conidia which did not fuse behaved similarly to those which paired, only the resulting germ-tubes and conidia were smaller and shorter. Three or more primary conidia have been seen connected, and double fusion between two has occasionally been observed.

Thus the normal mode of germination is for the spore to produce a stout promycelium bearing a tuft of primary conidia at its apex, and each of these conidia or the conidia united in pairs to produce a single secondary conidium, which puts forth a slender germ-tube to infect the wheat plant.

We must carefully distinguish, however, between what takes place in water or in moist air and in a nutrient solution. While the spores germinate freely in water, they do not succeed in a nutrient solution. Brefeld therefore first germinated the spores in water up to the formation of primary and secondary conidia, and then added a nutrient solution. Both primary and secondary conidia produce germ-tubes which develop into a much-branched mycelium, just like a tuft of mould, the hyphae of which are exceedingly fine. On the aerial branches numerous short lateral shoots are formed which swell up at their ends and become crescent-shaped conidia (Fig. 5*d*). These are easily detached, and again give rise to a tufted mycelium capable of producing further conidia in the manner already described, and this continues as long as the culture is maintained in the nutrient solution. No conjugations or fusions occur among these conidia. The branches of the mycelium which are given off in the nutrient fluid do not produce conidia, but grow outwards until they reach the air, when they produce terminal conidia or remain sterile, in which case the hyphæ are septate and appear empty.

Adaptations to Unfavorable Conditions.

This account of germination would not be complete without referring to the curious adaptations which Brefeld has observed to occur during germination, in order to provide against or to escape unfavorable conditions.

1. If the spores are submerged or the detached conidia fall into water, they only produce a germ-tube which must either enter the wheat-plant or die. The spores do not produce primary conidia, nor the primary conidia secondary conidia, because it would be a useless waste of energy, as they would be sure to perish in the superabundant moisture.

2. But if the spore germinates in water and the promycelium at length reaches the air, conidia are formed which become detached and are free to be distributed by the wind.

3. If the detached and paired conidia happen to germinate in moist air, they invariably produce secondary conidia, which are minute and easily detached, and may readily be carried by the slightest breath of air to a distance.

4. If these secondary conidia reach a place sufficiently moist, they produce a germ-tube for the infection of the wheat-plant, but if there is not sufficient moisture, they give off another conidium at one side, and so on until eventually they may either produce a filament which will enter a wheat-plant or die of exhaustion.

5. If nutriment is added to the water in the shape of organic matter, each primary and secondary conidium is capable of producing filaments which ultimately form a mass, like a tuft of mould, visible to the naked eye. The aerial branches develop sickle-shaped conidia, which are easily detached and readily distributed, and again give rise to a tufted mycelium bearing conidia, and so on. This shows how the conidia may be preserved in an active condition where organic matter is present. If there is sufficient moisture the conidia will germinate, and instead of perishing, if there is no wheat-plant at hand into which they may enter, they will absorb nourishment and grow like a mould and produce secondary conidia, which may, in their turn, either germinate or remain dormant according to the amount of moisture.

It is interesting to note that while Ustilago only produces spores in the host-plant, Brefeld succeeded in producing spore-like bodies with Tilletia in artificial cultures. Under these conditions the conidia give rise to hyphæ, which, after growth in length has ceased, begin to thicken in a moniliform manner, and then transverse septa are formed which isolate the rounded cells. After becoming free, they grow no more, but concentrate their contents and thicken their membrane, gradually assuming a dark colour and net-like markings on the walls. Although so far developed, they did not germinate when placed in suitable solutions.

There are thus two stages in the life history of this smut to be clearly distinguished—the *parasitic* stage, starting from the period of infection up to the time when spores are produced, together with conidia and secondary conidia, and the *saprophytic* stage, commencing with the germination of the conidia in a nutrient solution and producing conidia in damp air which are capable of infection.

Although the conidia arising from the promycelium and those produced from the mould-like mycelium are distinct in their mode of origin and in their shape, yet they have much in common. The former arise as a whorl at the apex of the promycelium and are generally elongated and filiform, while the latter are always formed singly from a hypha, and are shorter, thicker, and sickle-shaped. But in a nutrient solution, Brefeld has shown that both conidia form a mycelium, and when a number of cultures are made in water, those produced by the hyphæ assume all sorts of transition shapes, from the elongated filiform to the typically sickle-shaped.

Duration of Germinating Power.

The spores produced in the ovary retain their power of germination for two or three years at least, and Liebenberg[1] states that he has germinated them after eight-and-a-half years, of course after being kept under dry conditions. Since these dry conditions do not exist under ordinary cultivation for an entire season, it may safely be assumed that if a change of crop after

wheat is followed, the smut spores in the soil will have germinated and died, and if two years are allowed to elapse before wheat is again sown the chances are entirely against any smut spores having survived. Even the smut-balls would be broken up by that time in the ordinary operations of working the soil, or even by the slow movement of water in the soil. An experiment bearing on this was carried out with unbroken smut-balls in the soil to see if the spores were disturbed. Clean seed wheat was planted by hand in two rows alongside each other, in one of which the seed was pickled with bluestone and the other not, and unbroken smut-balls were planted close to the grains in each row. The result was that the plants were all clean in the pickled row, while in the unpickled several plants were bunted, thus showing that the smut-balls in the soil, even when undisturbed by the plough, can infect the seed wheat when not pickled.

Infection.

The mode of infection has been investigated, among others, by Kuehn[1], who artificially infected the youngest seedling stage with the spores, and afterwards traced the course of the germ-tubes by means of sections. He found that both primary and secondary conidia were capable of infection, and that the germ-tubes penetrate the epidermal cells directly through the walls, always in the neighbourhood of the lowest node. Just as the young seedling emerges from the grain, it is then in the most susceptible condition, and it may be attacked at any point up to the first joint, which is sometimes called the tillering point. The first joint is always beneath the surface of the soil, when the grain is drilled or harrowed, and not lying on the surface of the ground. Above that the plant cannot be infected, because the cuticle is too tough to allow the penetration of the delicate germ-tube. Therefore, unless the bunt spores were sown with the seed or existed in the soil, there is no possibility of infection. Once the germ-tube has entered the young seedling a mycelium is formed, which, if it reaches the growing point, keeps pace with the lengthening plant, chiefly growing among the loose cells of the pith, without interfering to any perceptible extent with the healthy growth of the plant, and finally reaching the ovaries, where spores are formed. It is thus seen how the parasite has conquered the host-plant in the long run, for just at the critical time, when the wheat plant is about to store away in the ovary for the benefit of the young embryo all the valuable materials accumulated during the growing period, the fungus enters in and appropriates them, rapidly growing at their expense, and forming a network of delicate branching hyphæ, which give rise to the innumerable dark-coloured spores.

Since infection only occurs in the young seedling by means of spores attached to the seed or by spores derived from smut-balls in the soil adjoining the seed, and since these spores are known to be destroyed or their germination prevented by bluestone solution, formalin, or hot water, the reason for steeping the seed before sowing is evident, while at the same time it is not seriously affected by the solution employed, particularly the two latter.

Artificial Infection of Seed.

Since a number of the plots were artificially infected, and as it is the usual way of testing susceptibility to the disease, it seemed desirable to see if different results were obtained, according as the spores were applied wet or dry and in larger or smaller quantities to the seed. The Wallace variety of wheat was chosen, and one plot was sown without infection as a check, while another was infected and treated with bluestone for comparison. When applied wet the spores were made into a paste with water, and the

grains rolled in this until they were quite black; when applied dry the grains were simply rolled in the dust from the crushed smut-balls until they looked as if coated with soot. The results are given in the following Table :—

TABLE IV.—INFECTION WITH SPORES APPLIED WET AND DRY AND IN VARIOUS QUANTITIES.

Plot.	Infection.	Stools.		Per Cent. Bunted.
		Bunted.	Clean.	
22	Spores applied dry—1 smut-ball to 100 grains	42	32	56.75
23	Spores applied wet—1 smut-ball to 100 grains	50	36	58.14
24	Spores applied dry—1 smut-ball to 5 grains	59	16	78.66
25	Spores applied wet—1 smut-ball to 5 grains	73	17	81.1

As far as conclusions can be drawn from a single experiment, the wet infection was a little more effective than the dry, and the increased quantity to a given quantity of seed decidedly increased the chances of infection, as might have been anticipated. Since this experiment was carried out I have come across the record of a somewhat similar one made by Gleichen as far back as 1781, and for the details of which I am indebted to a suggestive Bulletin on the "Smut of Wheat and Oats," by Professor Arthur. Gleichen, who seems to have been the first to test the method of infection experimentally, soaked one lot of seed in water and then rolled it in smut spores until completely coated, while another lot of seed was rolled in smut without previous wetting. The results are given by him for clean and smutted heads, and not for stools, but still they may be compared in a general way with those already given.

	Good Heads.	Smutted Heads.	Per Cent. of Loss.
1. Wheat sowed wet with Stinking Smut ..	178	166	48.
2. ,, ,, ,, ,, ,, ..	40	59	59.5
3. ,, ,, dry ,, ,, ..	102	35	25.5
4. ,, ,, wet ,, ,, ..	48	14	22.6
5. ,, ,, ,, ,, ,, ..	339	188	35.6

In the four trials with wet seed there was a loss of 41 per cent., and in the single trial with dry seed 25½ per cent.; so that the wet infection was here also the most effective.

THE SPORES AFTER HARVEST.

This is usually spoken of as the wintering of the spores, but as in our climate the wheat is reaped towards the end of spring and in early summer, the term is inappropriate. The sowing takes place in the autumn months, so that the spores pass the *summer* either on the grain or in the soil.

It is generally recognised that the threshing machine has a deal to do with the scattering of the spores and the dusting of the grain. When a wheat stack infected with bunt is being threshed, the beaters of the drum will break the bunt balls, and consequently the spores in countless millions will be scattered by the wind, and the wheat coming down into the bags will also be dusted with them. When the same threshing machine is used for another stack, which may be free from bunt, there are plenty of spores left about the machine to infect a new lot of grain. The grain in the bags will necessarily be stored in a dry place during the summer, and the spores cannot germinate until moisture is supplied to them when they are sown in the soil. It is well known that such seed dusted with spores and kept dry during the summer will produce bunted wheat in the succeeding crop if not treated, and even if the seed is kept dry for three years in a bag the spores will germinate and cause the disease all the same. Clean seed may also be contaminated by passing through a seed drill which has been used for bunted wheat, and the sacks in which the seed is stored may also be a source of infection. They should be disinfected by dipping in the solution used for treating the seed wheat, say 1 lb. of bluestone dissolved in 5 gallons of water, even although the wheat has been treated, for the seed may be reinfected through dirty bags.

But if the spores were exposed to the vicissitudes of the weather, as in the case of those falling upon stubble ground from the last year's crop, would they live and infect the new crop? Bolley[3] carried out experiments to settle this point, and he found that when the seed was treated to prevent any infection from that source, in no case were there any smutted heads. He considered that the spores, having germinated, the conidia, even although in the ground, were so minute that the probabilities were against their being in the proper position to infect the young wheat plant at the proper time. In every case where the seed was pickled there were no smutted heads, even although the soil was smutted. The results of these experiments show that spores falling to the ground lose their vitality the first season; but it is known that when bunt-balls remain unbroken in the ground and are broken the second year the spores may infect the young wheat plant.

Re-infection of the Seed after Treatment.

Reference has been made to the danger of re-infecting the treated seed by returning it to smut-infested bags, or sowing it by means of a seed drill not properly cleaned. In the case of bluestone, a thin film of the solution coats the grain, when it is properly soaked, and this is known to protect it against infection from spores on the grain itself, and from bunt-balls in the soil. But what happens when the grain receives a fresh coating of spores after treatment, either from broken bunt-balls or dirty bags, is a natural question to ask. This has been investigated by the late Mr. Farrer, and our own experiments are at present under way, the results of which will be available later.

As early as 1899 Farrer[2] commenced experiments with various fungicides for the treatment of stinking smut, and he found it necessary, at the same time, to test the effect produced by bunt-balls left among the grain and sown with it. In treating the seed, if the bunt-balls are not removed in the process, they are likely to be broken in the subsequent handling of the grain, and possibly infect it afresh, even although all the loose spores on the seed may have been destroyed.

The first experiments were designed to ascertain whether, and to what extent, the bunt-balls when crushed and treated with fungicides were capable of infection. The seed used was free from spores to begin with, and taken

from a crop also bunt free. Only two experiments were made with formalin. In the one the seed was infected from balls soaked for five minutes in a solution of strength 1 in 109 of water, and in the other the strength was 1 in 207 of water. In the first case the plants were all clean, and in the second 48.3 per cent. were bunty. But since the strength of formalin required to destroy the infective power of the crushed bunt-balls probably killed 73 per cent. of the plants treated, as shown by another experiment, it was evident that such a strong solution could never be used in practice. Several experiments were made with bluestone solution of various strengths, and they all showed a high proportion of bunty plants, ranging from 61 to 90 per cent., even although the balls had sometimes been soaked as long as 45 minutes. To take one experiment in which the strength used and the time taken was reasonable: The seed was infected from balls soaked for five minutes in a solution of 1 lb. bluestone in 4 gallons of water. The result was that 77 per cent. of the plants were bunty.

In the next series of experiments the treated and untreated bunt-balls were placed in the soil at the time of seeding. Untreated bunt-balls were placed in the bottom of the drill, at 1 inch, $\frac{1}{2}$ inch, and $\frac{1}{4}$ inch respectively from each wheat seed, and on one side of it only. The result was that infection occurred at the various distances, and the nearer the bunt-ball was to the seed the greater the infection. This varied from 4 to 17 per cent., and in one case there was no infection at all.

Bunt-balls treated with formalin, as in the previous experiments, dried and placed in the bottom of the drill, $\frac{1}{4}$ inch from each seed and only on one side of it, produced no infection. When bluestone, however, was used, the bunt-balls being soaked in a solution of 1 lb. to 4 gallons of water for five minutes, then dried and placed in the bottom of drill, it was found that when placed 1 inch from each seed there was $1\frac{1}{2}$ per cent. of bunty plants, and when $\frac{1}{4}$ inch from each seed, a little over 6 per cent. These experiments show that, if unbroken bunt-balls are contained in the seed after treatment, they are liable to be broken subsequently and infect the grain, and even if unbroken may infect adjacent untreated plants if sown with the grain.

In 1900[3], these experiments were continued, but only one is recorded relating to infection after treatment; and it is very suggestive as to the protective effect of bluestone solution. Minnesota Blue Stem was the variety chosen. The grain was soaked for five minutes in bluestone solution of a strength of 1 lb. in 4 gallons of water, then dried, and afterwards infected. The result was that $1\frac{1}{4}$ per cent. of the plants were bunty, while grain of the same variety taken from the same bulk, infected without any treatment, yielded 12 per cent. of bunty plants. The coating of bluestone on the seed evidently prevents the germ-tube of the fungus penetrating inside to any great extent.

In 1901, further experiments were made, and Farrer[8] records the results of infections after treating different varieties of wheat with bluestone, and then infecting the grains after drying. Purple Straw, Farmer's Friend, and Allora Spring were tested, the grains of each being soaked for five minutes in a 2 per cent. solution (1 in 50), then dried and infected. The percentage of bunty plants varied for each variety. In Purple Straw there was no infection, in Farmer's Friend nearly 2 per cent., and in Allora Spring nearly 9 per cent. The date of planting for all of them was 10th July, and Allora Spring alone was tried later, planting on 2nd August, and using a slightly stronger solution of bluestone over 3 per cent. (1 in 30). Two different plots yielded as nearly as possible the same percentage of bunted plants, viz., 19.74 and 19.77. The results here are rather discordant, and Farrer himself confesses

that he cannot account for the inferior protection against infection Allora Spring received when treated with a stronger solution and planted later.

In 1902[8], the experiments were continued, but the drought which prevailed and the excessive dryness of the seed bed at the time of planting were not favorable for obtaining normal comparative results. Yandilla was the only variety chosen, and the seed was soaked for 4 minutes in a $2\frac{1}{2}$ per cent. solution of bluestone (1 in 40), then dried, and afterwards infected. A second similar experiment was tried, the only difference being that the bluestone was dissolved in water to which a little gelatine had been added to see if a thicker coating would be formed on the grain, and thus protect it all the better against infection. The planting was done as late as 3rd September, and the percentage of bunty plants was a little over 4 and 8 respectively. The addition of gelatine did not add to the protective qualities of the bluestone solution.

It is evident from these experiments that grain may be re-infected after treatment, and every precaution should be taken to prevent this re-infection. The principal source of danger arises from smut-balls, which are liable to be broken in the seed drill, but no sample of wheat containing smut-balls should be used for seed purposes, and any stray ones should be skimmed off in the process of pickling.

Proportion of Smutted and Sound Stalks in same Stool.

It is commonly stated that when a plant is infected with stinking smut all the ears are generally affected, and that the cases are exceptional where smutted and sound stalks occur in the same stool. But a lengthened experience in Australia has led me to the opposite conclusion, viz., that it is less usual to find a stool in which all the ears are bunted, and it will be satisfactory to give examples bearing out this contention. This occurred during the past season at all the stations where bunt experiments were being conducted, but actual figures will be given. At Burnley, Dexter wheat was infected with bunt-spores—one plot with those of *T. levis* and another with those of *T. tritici*. At the end of the season I selected ten stools with bunted ears at random from each plot and counted the number of ears on each, separating them into bunted and clean. The following table gives the result :—

Table V.—Bunted and Sound Ears in each Stool of Dexter Wheat.

Stools.		Stalks.	Clean.	Bunted.	Stools.		Stalks.	Clean.	Bunted.
Infected with *T. levis*	1	8	6	2	Infected with *T. tritici*	1	20	14	6
	2	16	13	3		2	8	3	5
	3	14	10	4		3	7	3	4
	4	15	11	4		4	20	7	13
	5	27	18	9		5	9	6	3
	6	23	21	2		6	12	3	9
	7	10	8	2		7	13	6	7
	8	12	8	4		8	15	13	2
	9	10	5	5		9	14	10	4
	10	12	10	2		10	8	6	2
Totals	10	147	110	37		10	126	71	55

It is seen from the above Table that every stool was only partially bunted whether the spores of *T. levis* or *T. tritici* were used, and that in both cases

there was a greater proportion of clean than bunted. With *T. levis*, 75 per cent. were clean, and with *T. tritici*, 56 per cent., so that the same plant, as a rule, produces both sound and smutted heads.

I next examined a large number of bunted plants to try, if possible, to find one in which all the ears were affected. Federation was the variety chosen, because it is specially liable to bunt, as it was infected with *T. levis*, and 72 per cent. were diseased. On examining 20 diseased stools at random, as in the case of Dexter, the result was as follows :—

TABLE VI.—BUNTED AND SOUND EARS IN EACH STOOL OF FEDERATION WHEAT.

Stools.	Stalks.	Clean.	Bunted.
1	14	1	13
2	16	1	15
3	9	3	6
4	11	2	9
5	20	0	20
6	9	0	9
7	12	4	8
8	13	1	12
9	17	9	8
10	8	0	8
11	6	0	6
12	8	1	7
13	9	1	8
14	6	0	6
15	10	1	9
16	7	0	7
17	8	2	6
18	10	0	10
19	6	1	5
20	10	1	9
Total ..	209	28	181

Out of twenty plants, there were seven entirely bunted, and only 13 per cent. of clean ears. When the variety is particularly susceptible, there may be a considerable proportion entirely bunted, but under our conditions, a mixture of smutted and sound ears in the same plant is the more common.

GRAINS OF WHEAT PARTIALLY BUNTED.

The normal course of the stinking smut fungus is to produce its spores in the ear, and in every ear of the stool attacked, as well as in every grain of the ear, and the contents of each grain is converted into a foetid mass of spores. But when a number of diseased specimens are examined, it is found that the spores may occasionally occur on the stem, as well as in the ear, and that it is not at all unusual in certain seasons for only some of the ears in a shoot to be bunted, while a number of the grains in the affected ear may escape, and even the grain itself may be only partially diseased. I have not, personally, found bunt-spores elsewhere than in the ear, but Berkeley[1] records an instance of a streak of bunt appearing on the stem. The plant to which he refers in the following sentence was grown from a grain infected with the spores of bunt :—" In one of the bunted plants, not only the ear was diseased, but there was a streak of bunt upon the stem, in which the foetid smell and

peculiar structure were not to be mistaken, a circumstance which I have never before observed, nor am I aware that the fact has been noticed by others."

The occurrence of bunted and clean ears in the same stool has already been fully referred to in Chapter VIII., and bunted and clean grains in the same ear are illustrated in Plate II., B and C.

That the grain of wheat itself in a diseased ear should be only partially bunted, is regarded by some as an impossibility, nevertheless, two examples have been met with this season, confined to a single ear in each case, and one of them is here photographically illustrated. This belonged to the variety known as Cedar, grown at Dookie Agricultural College, and the one ear contained all the gradations of sound, bunted, and partially bunted grains. The three partially bunted grains were partly translucent and partly opaque and dingy, indicating, apparently, the diseased and healthy portions. On making transverse and longitudinal sections of the diseased grains, fungus filaments and numerous spores were found interspersed between the outer skin and aleuron layer on one side, while the other portion was of the normal character and filled with starch granules. (Fig. 10.) In a longitudinal section, the embryo was seen to be quite intact and partially surrounded by the numerous spores, some of which were still in the early stage with fungus filaments attached. The species belonged to *Tillitia tritici*, with the spores of which the plants had been originally infected. The other specimen was found on Genoa, grown at Burnley, and the ear contained sound and entirely bunted grains, and only one partially bunted. This variety was infected with *T. levis*, so that both species of smut produced partially bunted grains.

I have had a partially bunted grain photographed, both as it naturally appeared, and in section, because Bolley[3] has stated very distinctly and emphatically, after making hundreds of sections of apparently sound grains, that "In a crop of stinking smut, the grain product is made up of solid grains and smut balls only. In other words, there are no grains which are partially smut and partially flour." I grant that such an occurrence is exceedingly rare, but it shows how difficult it is to prove a negative.

Fig. 7.—Section of Clean grain × 14.

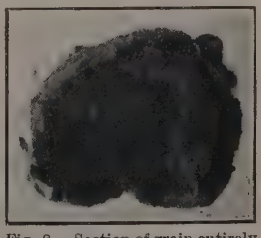


Fig. 8.—Section of grain entirely bunted × 14.

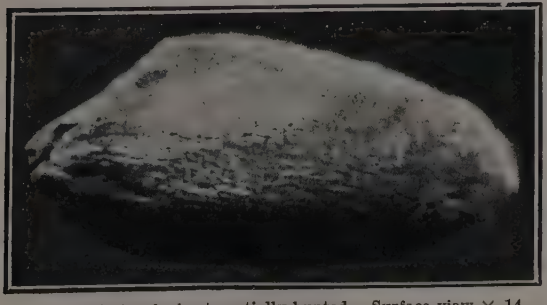


Fig. 9.—Grain of wheat partially bunted. Surface view × 14.

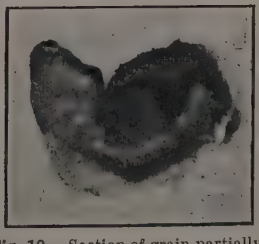


Fig. 10.—Section of grain partially bunted × 14.

Conditions favouring the Disease.

There is no doubt that bunt is more prevalent in some years than in others. In the season of 1898 it was so prevalent in Victoria that it was estimated to have caused a loss on the year's crop of £50,000. In 1908, with a record harvest, there were certain districts, such as the Wimmera, where the value of the crop was considerably reduced from this cause alone. Ten years ago, the treatment of seed-wheat for smut was neither so general nor so well carried out as it is now, although farmers asserted that every precaution had been taken in the treatment, and even now there are some who neglect it altogether, or do it in a slipshod manner.

Heat and moisture are the two controlling factors in its development, especially the latter. It is generally considered that less moisture is required to germinate the smut spores than the wheat, on account of their much smaller size, hence it is a common practice in some districts to sow the seed unpickled in a dry seed-bed, but to pickle it after rain. In the one case, the insufficient moisture is likely to start the growth of the smut spores before the wheat, and in the absence of a host-plant, the germ-tubes shrivel up and die, while in the other, there is every probability of both germinating at the same time and infection is sure to occur. A cold and wet period immediately after sowing is more favorable to the growth of the bunt than of the wheat, and the tissues of the young plant, being soft and tender, there is often a larger proportion of bunt than usual. But in discussing the relations between the nature of the season and the prevalence of bunt, there are no definite experiments to guide us.

Effects upon the Crop.

When the smut appears in a crop, the farmer generally considers his loss as being entirely due to the ears destroyed by the fungus and to the depreciation in price per bushel for the remaining sound wheat, but it has been shown by Bolley[3] particularly, that smutted ears are only an indication of more widespread damage. Thus it was found that in stools with only one or a few ears affected, the smut fungus was in all the straws, even when the heads were sound. Further, in untreated wheat paddocks where only about one-third or one-fourth of the crop had actually smutted heads, it was difficult to find a stool or a straw free from the fungus, explaining why the crop was materially reduced beyond the evident indications. Then the growth of the straw may be seriously interfered with, as well as the formation of the heads, for it has been observed that on stools bearing smutted ears there are often several unheaded straws. Kuehn[1] even found that, where smut infection was very bad, young plants might die back completely. Where the straw is completely formed, the heads may still be poor, for just at that period when the grain is about to be formed, if the fungus is present, there is likely to be a shortage of supplies. As we remarked in connexion with the rust-fungus, "In the actively growing and feeding period of the plant's life, it is apparently able to provide for the wants of the fungus as well as its own, and therefore its vitality is not seriously affected. But when the second period of forming and ripening the seed arrives, when feeding is gradually ceasing, and the accumulated materials are being transferred to the seed, then the fungus draws upon the plant's capital, crippling its energies, and checking the movement of the food materials to the seed." If the fungus filaments are not sufficiently robust to give rise to the spore-forming hyphae and invade the grain, they are still capable of diverting food material from its natural destination—the ear.

Diseases produced in Animals.

The disastrous effect upon the crop is not the only thing to be considered, for the smut possesses poisonous properties which render the flour contaminated with it dangerous to human beings and the straw or chaff eaten by cattle is also injurious. In seasons when this disease of wheat is prevalent, owing to the seed-wheat not being treated properly, there is a good deal of the chaff given to cattle and horses. Tubeuf[1], referring to this particular smut, remarks—"The symptoms in the few cases of disease observed do not agree very closely. A paralyzing effect on the centres of deglutition and the spinal cord seems to be regularly present. As a result, one generally finds a continuous chewing movement of the jaws, and a flow of saliva, also lameness, staggering, and falling. Cattle, sheep, swine, and horses are all liable to attack."

More recently, Güssow[1], in the *Journal of the Royal Agricultural Society of England*, has been writing in a similar strain. "The smut fungi (*Ustilagineae*) of our cereals and grasses, especially the fungus known as bunt (*Tilletia caries Tul.*) have proved extremely dangerous to animals of the farm. After feeding on hay which contains the spores of these fungi (often in enormous masses so that they form clouds of black dust when the grain passes through the machine), inflammation of the mucous membrane, laboured action of chewing, flow of saliva, and occasional abortion have resulted."

According to Smith[1], fowls have been fed with bunted wheat without any bad result, but that is not our experience here. At a poultry farm near Melbourne, carrying 650 Leghorns, about the beginning of March, the egg yield dropped in a few days from an average of 100 to 16, and that without any apparent cause, the fowls being given the usual feed with a good supply of meat. The wheat was examined and found to be smutty, and it was further found that the egg yield began to drop from the time this particular line of wheat was used. The use of the smutty wheat was at once stopped and now, at the end of March, barley, with a fresh line of clean wheat, has been tried, with the result that the egg yield has begun to improve and is steadily mounting up. At the end of three weeks, after the use of smutty wheat had been discontinued, the average yield of eggs had reached 80 per day. The smut in the wheat was the only cause that could be assigned for the unprecedented drop in the egg yield, as in every other respect the feeding was the same as usual and the weather was good at the time. In some cases, fowls have refused to eat badly smutted wheat, after being fed on it for several days, preferring an empty crop. Other poultry-keepers have had similar experiences of the injurious effects of feeding their birds on smutty wheat.

Experiments were also conducted with pigeons, to see the effect of feeding with clean as compared with smutty wheat. They were kept under exactly the same conditions for twenty-two weeks, the only difference being that the one pair was regularly fed with clean wheat, while the other had a particularly bad sample of smutty wheat. During that period seven eggs were laid as the result of feeding with clean wheat, while the other, fed on smutty wheat, only produced two eggs. Both pairs were in good plumage at the start, but at the end one pair retained their lovely plumage, and were in good condition and fat, while the other pair were in poor condition, and the feathers all standing up. The mouth inside was quite black from the smutty wheat, and there was a danger of disease being produced in time, such as cancer in the throat. Experiments with a single pair of pigeons are too limited in their scope to allow of final deductions being drawn. But it may be noted that the pigeon fancier, from whom the birds were received and to whom they were

returned, found that all his fifty pigeons were laying, with the exception of the pair fed on smutty wheat, even although they were now being fed on clean wheat.

Legislation Relating to Plant Diseases.

A cargo of wheat was shipped to Victoria from Tasmania in which not only every grain was densely coated with the spores of stinking smut, but the balls containing millions of spores were freely scattered through it. Although there was plenty of smutty wheat within our own borders, it was not deemed advisable to admit it from a neighbouring State, so it was refused admission under the Health Act as being unfit for use as human food in that condition. But the importers, taking advantage of the absence of legislation on the subject, labelled it as "Fowl's feed," and there was no law to prevent this. Here was evidently a case where it was necessary to protect ourselves against the introduction of grain which was proved to be injurious even to fowls, not only as regards their general health, but seriously interfering with their laying capacity. Accordingly a proclamation was issued under the authority of the Governor in Council, whereby this particular disease was brought under the Vegetation Diseases Act, and thus any further importations of that nature were rigidly excluded.

This instance clearly shows the necessity for each State having the power to protect itself, and prohibit the importation of diseased plants or parts of plants, and not only so, but for the Commonwealth to have the power of excluding any plants which might be the means of introducing disease into Australia. There are at present legal means in existence for accomplishing this end—the Vegetation Diseases Act in each State and the Quarantine Act for the Commonwealth as a whole.

Summary—Answers to Questions.

This particular smut has been treated at some length, because it is the form with which the farmer is most familiar, and it appeals to him as the type of smuts in general. Therefore, it has been deemed advisable, by way of summary, to conclude by clearly stating a number of questions which he often, consciously or unconsciously, asks himself, and answering them as far as observation and experiment will permit.

It is of fundamental importance for him to realize at the outset that the smut plant is a fungus which develops from spores that are the equivalent of seeds in other plants so far as the propagation of the species is concerned, and that this plant grows as a parasite within the wheat plant until it reaches the grain, and there produces its fruit or masses of spores (ball smut), similar to those from which it started. In order to grow and develop properly, this smut plant is dependent on surrounding conditions, just as much as the wheat plant itself, and if we understood those conditions, it would explain why the spores sometimes germinate and sometimes do not, why the smut plant sometimes reaches maturity and forms its spores, and sometimes does not, just as the seed-wheat may or may not germinate and the seeedling may or may not reach maturity.

It is also of prime importance to remember that the wheat is only infected in the seedling stage, just as the young plant emerges from the seed beneath the surface of the soil. Consequently, no infection can come through the air, unless, indeed the grain germinates upon the surface of the ground, and when it is properly planted, only the spores adhering to the seed or smut-balls adjoining it can produce the disease. The farmer sometimes sees, or fancies he sees, smut spores upon his fences, and when he has treated his wheat after a fashion, and the smut still appears, he tells you that it was blown from

the fences. But when the wheat plant is above ground, it is proof against infection from bunt spores, so that there must be some other reason for the failure of the treatment.

There are questions sometimes put by the farmer, however, which cannot receive a definite answer, because his experience does not always take note of the accompanying conditions, and because his love of paradox sometimes overrides his experience. I am often asked by farmers, "Why is one part of a paddock of wheat smutted and the other not, the seed in each case being treated properly and sown at the same time?" It all depends here on what is meant by proper treatment of the seed, as it is implied by the question that the fault must be in the soil. But it is found by experiment that when the seed is properly treated with bluestone solution and all the smut balls removed, there is no smut in the crop, even although spores of the smut may be in the soil from a previous crop or from self-sown wheat. Then the farmer almost invariably upsets any answer you may give by adding that the next season things were reversed, the clean part of the paddock being smutted and the other not, even with the aforesaid proper treatment. Bearing in mind that there is no fungus disease known which can be more readily or more absolutely prevented than this smut, we will now propound a few of the questions which arise in connexion with it.

1. *Is the smut of wheat, oats, and barley the same?*

No, they are quite distinct, for the smut of wheat cannot infect oats or barley, nor can the smut of oats or barley infect each other or the wheat.

2. *Why does bunt sometimes appear in a paddock when the seed is supposed to be properly treated?*

This may be due to various causes, such as returning the treated grain to bags which have not been disinfected and thus re-infecting the grain; or sowing the seed with a drill which has not been properly cleaned. It may be, however, that the smut balls had not been skimmed off in the process of pickling, and being crushed in the drill, the seed is infected.

3. *Will the bunt spread from one paddock to another or from one plant to another, like the rust, when the crop is growing?*

Since infection occurs in the seedling stage only, and the germ-tubes penetrate at the point where stooling occurs, and that is beneath the ground when the grain is covered with earth, there is no possibility of the disease spreading from one growing plant to another.

4. *Should seed-wheat be used from a crop known to be bunted?*

Decidedly not, for there is a strong probability that the grain will not be so plump as if perfectly healthy. A crop may have but comparatively few actually smutted ears and yet give a much reduced yield and a poor quality of wheat, because the smut was in the straw and affected the yield, although it did not reach the ears before maturity of the grain.

5. *Will spores lying on or in the ground from last year's crop infect the next?*

This question of infection from the soil often crops up, but since it was found by repeated experiments that properly treated grain, even although grown on very smutty ground was free, it may be concluded that soil-infection practically does not occur. I say practically, because there is a possibility of stray infection taking place when there are numerous spores around the germ end of the seed, where the young plant bursts through.

6. *May bunt originate from self-sown wheat?*

Self-sown wheat is rarely affected by bunt, still it may occur in some seasons. I have usually seen self-sown crops perfectly free, and have also found

a little, but not in sufficient quantity to injure the sale of the wheat. It is generally stated that it is the heat of the sun in summer which kills the bunt spores on self-sown wheat, but Farrer[5] showed that the rains and the dews may also cause the spores to germinate, and having no germinating wheat plants to penetrate, they soon perish. The heat of the sun and the dews at night are likely to prevent the appearance of bunt in a self-sown crop, but if the interval between the harvesting of the crop and the sowing of the next, as well as between the ploughing of the land and the seeding is short, together with cool and dry weather, there may be some danger of infection. In the early days, many farmers used to expose on a cloth the wheat intended for next year's seed. They found that the weather—dews, sunlight, and hot dry winds—acting on the seed for a period of several weeks, killed the spores, or rather, they discovered that it gave a comparatively clean crop, without knowing the reason why.

7. *Why is there more bunt from the same seed in one paddock than another?*

There may be various reasons for this. The land may be fallowed in the one case and not in the other. It may also be more moist in one paddock than another, and thus favour the germination of the spores at seeding time. Actually wet soil would be inimical to germination. Whatever delays the first growth of the wheat plant will be favorable to the increase of bunt.

8. *Does the date of seeding influence the amount of bunt in the crop?*

Different conditions at seeding time are likely to affect the result. Bolley[3] carried out experiments to test this, sowing the same kind of seed on various dates of April, May, and June. He found that the untreated seed yielded the heaviest growth of smut in the earliest date, viz., April. "It was also observed, in all tests, that the number of smutted heads stayed quite approximately in proportion to the total number of heads, *the best crop of wheat producing the best crop of smut.*" I carried out an experiment with flag smut which shows that the date of sowing has a very decided influence. The seed was purposely sown on 24th April and 16th July, or nearly three months between, on land that had borne a crop badly affected with flag smut the previous season. The first was sown when the ground was dry, but there seems to have been no germination until the rain came, which germinated both the seed and the smut, for there were up to 14 per cent. of diseased plants. The later sown was about a month after the rain, and the ground was in excellent order, but the spores had evidently germinated and perished in the interval, for there was only about 1 per cent. of crop affected.

The weather and soil conditions enter so much into the result that a dry or a moist seed bed at the time of sowing, or a spell of warmth, or of frost at the time of germination, is bound to make a difference.

9. *Why are some varieties more liable to bunt than others?*

As afterwards more fully discussed, this may be due to the fact that the least liable variety germinates so rapidly that the smut plant is unable to reach the growing point of the wheat, and so dies, or there may be something in the tissues of the variety unsuitable to the growth of the fungus, and so the variety is said to have the hereditary or inherent quality of bunt resistance.

10. *When all the grains are equally inoculated with spores, why are some plants bunted and others not?*

It is quite a common occurrence for inoculated seed to be sown under similar conditions, and yet a number of the plants escape infection. It is not easy to answer the question, but a few considerations may help in this direction. First of all, the young seedling must be at the right stage of

growth in order that the germ-tube of the fungus may penetrate, and this period is of very short duration. Next, the germ-tube must grow and reach the growing point, or it would not be able to develop and produce the disease. But a main reason for some plants being attacked and others not lies in the fact that there are certain substances known as chemotactic substances in the plant which favour the entrance of the germ-tube of the fungus and its development inside. There are also substances which actually repel the germ-tubes, and it is the presence or absence of these substances which determines whether an individual plant will be attacked or escape. The seed from plants, however, which escaped infection in one season have been sown the next and found to succumb.

11. *Why are some plants partially bunted—only some of the ears being affected and not all?*

It often happens that only the secondary or late ears are affected, the others being clean, and this might arise from the fungus filaments at the base of the plant only reaching the growing point of the slow and late developing plants, while the others escaped. In other cases, where the fully developed ears were bunted, the germ-tube had evidently reached the growing point of the seedling, and the mycelium had kept pace with the growing plant.

12. *Why are some ears only partially bunted?*

Under ordinary conditions the whole of the grains in an ear are affected, but in certain seasons it is not unusual to find ears in which some of the grains are bunted and others clean (Plate II., B). It may be that one side of the ear has escaped, but usually the sound grains are interspersed among the bunted. In one particular case the lower grains were all bunted, then about the middle an occasional one was clean, and at the top both smutted and sound occurred, the topmost grain, however, being diseased (Plate II., C). The normal condition is that all the grains in an ear are attacked, and when some escape it can only be owing to the spore-bearing hyphae failing to reach these particular grains. It might be thought that the grains which escape the invasion of the fungus to form spores had some resisting power, but when the clean grains in a partially bunted ear were infected and sown they produced bunty plants, showing that there was nothing in the grain itself to account for its escape.

13. *Why are some grains of wheat only partially bunted?*

This was a comparatively rare occurrence, only appearing in one ear of the variety known as Cedar, grown at Dookie, and in one ear of Genoa, grown at Burnley. In the latter ear there was only one grain partially bunted, three entirely bunted, and all the rest free. In the partially bunted grain the fungus had evidently exhausted itself in producing its spores only on one side, and why the whole of the starch was not utilized, as is usually the case, in the formation of spores, might be due to the slow growth of the fungus, or its late entrance into the grain, as evidenced by the embryo having had time to develop.

In fact, in all these cases, whether it is smutted and sound plants on the same stool, or smutted and sound grains in the same ear, or even when the grains are only partially smutted, the probable explanation is the same, that by some accident of growth the fungus did not undergo its full development, and was unable to reach all parts of the plant as usual.

CHAPTER XIII.

Loose Smut of Wheat.

(*Ustilago tritici* (Pers.) Jens.)

Of the three different species of smut known on the wheat plant in Australia this is one considered the least injurious, but it may be present to a considerable extent and yet overlooked, because the stalks affected are usually stunted. Like the oat smut it is produced in the ovaries, and destroys the various parts of the flower, so much so that at harvest time only the bare stalks of the ears remain after the spores have been blown away. It is distinguished as loose smut from the powdery nature of the spores, or flying smut, from the way in which it flies when blown, and the ears are often spoken of as "snuffy ears" by the farmer (Plates III., VI.). It differs from the much more common stinking smut or bunt in having no objectionable odour, and the loose dusty mass of spores ripen and are blown away while the wheat plant is in flower, instead of remaining and filling what would otherwise be the grain with an evil-smelling compact mass of spores, only broken up and scattered when being harvested or threshed.

When a stool is affected with loose smut, the stalks are generally of a purplish tint, so that they can be readily picked out from among the general crop. The same has been observed in the naked smut of barley, but it is not particularly so in the case of loose smut of oats. This purplish colour is natural to some wheats, such as Purple Straws, but it occurs in other varieties as well when smutted. It is sometimes attributed to premature ripening, the food materials in the straw not being completely converted into food for the embryo. But I am inclined to think, as it occurs particularly in those cases where flower infection takes place, that the young embryo is influenced in some way by the fungus filaments present in the grain, and this is afterwards shown in the peculiar colour of the straw.

Unlike the loose smut of oats, it is not uncommon to find stools with both smutted and sound ears.

Germination.

Kellerman and Swingle[3] and Herzberg[1] have described the germination of this species, and I have found it to germinate readily in water and in a nutritive solution. After being kept for five months the spores germinated at once. In water they germinated fairly well in 24 hours, and in three days there were copious branchings. The main germ-tube was nearly always slightly curved, although it might grow out quite straight. The numerous branches might arise either beneath a septum or opposite to each other, or sometimes a protuberance opposite to a septum grew out into two branches alongside of each other, above and below the septum.

In a nutritive solution such as hay infusion, after eighteen hours a slender germ-tube was formed, and it is generally characteristic of it that it curves in a sickle-shaped fashion. After 24 hours branches are freely formed, and the whole grows out into a much-branched mycelium without the formation of any conidia. This peculiar curvature of the branches is so striking that when copious branching has taken place the whole resembles a loosely wound coil of filaments.

G. H. Robinson, Phot. Nat. Size.

LOOSE SMUT OF WHEAT

(*Ustilago Tritici.*)

Infection.

It has generally been taken for granted that the wheat smut, like the oat smut, only infected the young seedling, and that the fully-developed plant was immune. It was assumed that the spores fell to the ground, retained their germinating power there, and that they caused infection the next season in the young seedling. This view was rendered probable from the fact that in some of the smuts, as will be shown in the case of flag smut, the spores in the soil infected the young plant, so that treatment of the seed did not prevent the appearance of the smut. Another view was that the spores reached the flower and there remained on the seed which was formed until the next sowing season, but, unfortunately for this view, the spores only retain their germinating power for a few months. All these conflicting views were finally disposed of when Brefeld and Hecke carried out their conclusive experiments, and showed that infection took place through the flower and not through the seedling. Previous to this, however, it had been experimentally proved by Maddox, in Tasmania, that flower infection occurs.

It is well known to every agriculturist that, when grain is dressed for stinking smut or bunt, the dressings have no appreciable effect on loose smut, and in my experiments with bluestone and formalin treatments I have always found this to be the case. This fact can be easily explained when it is remembered that the source of invasion is from within, and it is not reached by the dressings usually employed. The mycelial filaments are so intimately bound up with the living cells of the embryo that the destruction of the one would involve the death of the other.

The only feasible measures for this disease at present seem to be to select seed from crops free from the disease, and at a sufficient distance from any diseased crop, so that air-borne spores could not be carried at least in any great quantity. Also, as in the case of rust, to endeavour to breed a race of wheat capable of resisting the disease. Quite recently the hot-water treatment of the seed has been found effective, both in Loose smut of Wheat and Naked smut of Barley.

CHAPTER XIV.

Flag Smut of Wheat.

(*Urocystis tritici.* Koern.)

This smut, as the common name denotes, is most commonly found on the leaf blades and leaf sheaths, but it may also occur on the stem and even on the chaff; but very rarely in the ovary, as it is seldom formed (Plates IV., VI.). Since it prevents the formation of the ear, this disease is very destructive in its effects, and in some seasons favorable to its development, such as that of 1906, the harvest was considerably reduced by it in several districts of Victoria. The serious nature of the disease and its widespread occurrence demanded a thorough investigation, and, as far as time and opportunity permitted, this has been done. Not only have Laboratory experiments been conducted as to the germination of the spores and the mode of infection, but field experiments are being carried out to determine how far special treatment of the soil or a suitable rotation of crops can mitigate the disease, for it has already been proved that the treatment of the seed so successful in the case of stinking smut does not prevent the appearance of the disease. The following account will give the present state of our knowledge with reference to this disease and the measures that have been tried to keep it in check.

Although it has been known in Australia at least since 1868, it was only in 1873 that Wolff[1] definitely determined the fungus causing it to be the same as that on rye—*Urocystis occulta*—but as it is afterwards shown to be biologically distinct from that species, the more striking differences between the two may here be given.

Stem Smut of Rye and Flag Smut of Wheat Compared.

It is the characteristic of *Urocystis* on the wheat that it principally attacks the leaf sheaths and the flag or blade, causing the latter to curl up and become variously twisted and distorted, while the ear is very seldom formed (Plate IV.). In the rye, on the other hand, the long grey streaks are formed on the flag without causing much distortion, and even in observed cases, where the whole plant was more or less affected, the lower and older leaves still retained their normal shape, only splitting up towards their tips in lines parallel with the streaks of the fungus and becoming frayed. But it is on the stems that the streaks are principally noticeable, where they run together, more particularly at the base of the inflorescence, forming one dense mass of black spores as the epidermis ruptures to expose them. Not only do the spores escape on the outside of the stem, but the tissue is ruptured on the inside, so that the cavity of the stem is more or less filled with the black spore-powder. The ear is generally formed, but arrested in its development, only becoming a sort of skeleton ear, and it usually droops, as the tissues of the stem immediately beneath it are more or less destroyed by the fungus (Plates V. and VI.). Hence the common names by which these diseases are generally known—the *flag* smut of wheat, and the *stem* smut of rye.

Another feature of the flag smut of wheat is that all the stalks in a stool are often affected, while in the rye, as far as my observation goes, this is not the case. Thus, in one stool of rye there were eighteen healthy stalks and five diseased, and the healthy ears all produced the normal grain. In addition to these visible differences there are others which are microscopic, and are duly noticed in the technical description of the fungus.

G. H. Robinson, Phot.

Nat. Size.

FLAG SMUT OF WHEAT

(*Urocystis Tritici.*)

History.

The earliest record I can find of the prevalence of this disease in Australia is contained in the Report of the South Australian Commission on Diseases in Cereals in 1868. There it is unfortunately referred to under the name of "Black Rust," and even at that period it is spoken of as a disease with which the farmers were familiar.

In New South Wales Dr. Cobb[1] had referred to it in 1891 as being a serious plague, and remarked that "It is not rare for half the crop to be lost through its ravages, and a loss of 10 per cent. is common." In 1892 I first reported upon it at Rochester, in Victoria, where it had been prevalent for some time, and had caused considerable loss.

On making inquiries as to its occurrence in Queensland, I am informed by the Government Vegetable Pathologist there that only a single instance of it had come under his notice in 1906 in a wheat crop grown in the heavy soil of the Hodgson district. However, this does not imply that the disease was confined to this one spot, for he significantly adds—"that it may have been more prevalent than is indicated by this statement, since farmers are not in the habit of calling attention to affections in their crops until these are sufficiently pronounced to cause them some concern." In West Australia and Tasmania there is no record of it so far.

This disease was at first only known on wheat in Australia, but now it has been recorded on wheat in Japan in 1895 by Hori[1], and on wheat in India in 1906 by Sydow and Butler.[1]

Origin.

Although this smut first appeared, as far as known, on wheat in Australia, it does not necessarily follow that it originated here. It is always difficult to trace the early beginnings of a particular disease, especially after it has become rather widely distributed. It may have been introduced into Australia through the medium of the seed or chaff of rye, and particularly into South Australia where there are a number of German settlers. Mr. Summers, of the Agricultural Department, Adelaide, has kindly made inquiries, and informs me that it has long been customary for settlers on the hills to grow small plots of rye for early green feed. Once introduced, this smut might adapt itself to the wheat plant, in the absence of its regular host-plant—the rye—in sufficient abundance, and in such an extensive wheat-growing country as South Australia its spread would be only a matter of time. This, however, is only a surmise, as there is no record of smut on the rye. It is hardly necessary to do more here than refer to the popular notion that all smuts are practically the same, no matter on what plant they occur, and that the flag smut of wheat may easily have been derived from one of the others. It is quite possible that flag smut of wheat may have been derived from rye smut, which also occurs, although less frequently, on oats and barley, as it is closely allied to it in structure and habit, but that is something very different from saying that one smut may arise indiscriminately from another, even when they are as distinct in their structure and life-history as stinking smut and flag smut. There is another point worthy of consideration in regarding this smut as having probably been derived from that of rye, and that is the close affinity between the two host-plants. Rye is said to be more closely related to wheat than any other cereal, although differing in several particulars, and the same rust has been found on it, viz., *Puccinia graminis*, Pers., which Eriksson found to produce aecidia on the Barberry, just as in the case of wheat.

Symptoms and General Characters.

The first indications of the disease are seen on the leaves, where it forms long grey streaks at first running parallel with the veins, and the black powdery spores are set free by the rupture of the leaden-coloured epidermis. The ruptured skin and long black streaks suggested a kind of rust to the farmer, and so he called it "Black Rust." The ear is rarely formed, for what should

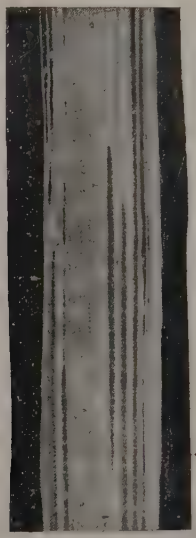


Fig. 11. Portion of Sheath showing elongated black lines caused by the fungus. × 2.

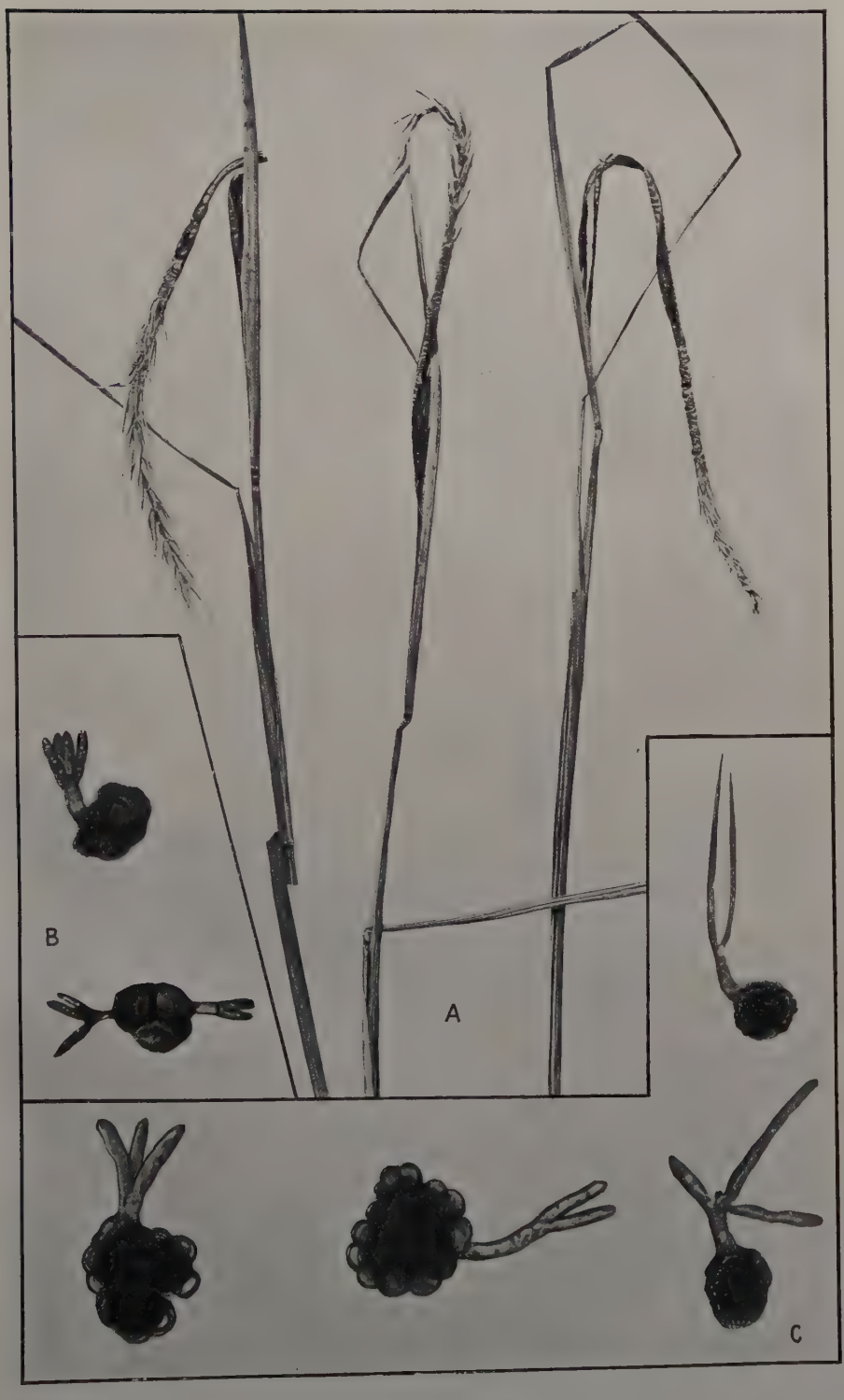
be the ear is generally only a twisted mass of diseased tissue as seen in Plate IV. Occasionally the grain is formed, but it is extremely small and shrivelled, and only in very exceptional cases have a few seemingly perfect grains been found. On trying to germinate some of these they all died within a few weeks.

The leaves generally become curled and twisted up, and the entire plant often withers before it comes into ear. All the stalks in a stool may be affected, which is usually the case, or only a portion of them. From the way in which the affected plants die down in the midst of an otherwise perfectly healthy crop the true cause of the shortage in the harvest is often not realized, but the curled and twisted and streaky leaves of the earless plants are sure evidence of this disease.

Effects.

In South Australia, where the disease has long been known in the wheat crops, it is regarded as being in some seasons quite as injurious as the rust itself. In Victoria as much as half the crop may be lost through it, and in New South Wales Dr. Cobb has shown it to be equally bad. It was observed in Japan that all the wheat plants in an area of about one quarter of an acre were entirely destroyed by it, but this was an exceptional case.

From the way in which some plants of a stool are affected—others not—and from the fact that the disease generally prevents the formation of ears, the farmer is often at a loss to know the true cause until his attention has been specially called to it. He knows that his crop promised earlier in the



× 500 and $\frac{1}{3}$ Nat. Size.

C. C. Brittlebank, Phot.

A—STEM SMUT OF RYE. B—GERMINATING SPORES OF UROCYSTIS OCCULTA. C—GERMINATING SPORES OF UROCYSTIS TRITICI.

year a much heavier yield, but the season is generally blamed for the shortage. As will be shown afterwards, the twisted and curled leaves breaking up and falling to the ground are the main sources of infection for next season, and it can readily be understood that where wheat is grown year after year and no precautions taken against this disease the effects are cumulative. This will account for the widespread and injurious effects of this disease in many wheat-growing districts.

Conditions favouring the Disease.

In the evidence given by farmers before the Commission on Cereal Diseases in South Australia in 1868, various conditions and causes were assigned for this disease. Early and self-sown crops were said to suffer most, and all loose and richly-manured lands were supposed to be very liable. Ploughing-in the straw was also said to encourage it, and early sowing, combined with a spell of dry weather, was sure to bring the disease. Hence late sowing and wet soil were recommended for its prevention, as it was generally understood the later you sow the less likely you are to have it.

Among Victorian farmers it is also held that dry sowing is more subject to the disease than wet, and one even went the length of saying that when wheat was sown in very wet ground there was no flag smut. The lighter ground is generally found to be the worst, and it is said that virgin ground, in districts liable to this disease, generally bears two clean crops while the third is attacked. This probably means that the disease has spread sufficiently in the third crop to make it noticeable to the farmer as being injurious.

The effect of early and late sowing, as well as of a dry and a comparatively moist seed-bed on the appearance of flag smut, was put to the test in 1907. Wheat was purposely sown on 24th April, when the ground was dry, on land which had borne a crop of wheat badly flag-smutted the previous season. There was practically no rain till June, when about an inch fell on the 20th. This rain seems to have germinated the seed-wheat and the fungus spores at the same time, giving thereby a heavy proportion of diseased plants, up to 14 per cent. Alongside the early-sown plots a second sowing was made on 16th July, about a month after the rain. The ground at sowing time was in excellent order, and it was a remarkable fact that at harvest the proportion of diseased plants, taking all the late-sown together, averaged only 1 per cent. The conclusion to be drawn from such a test is that early sowing in a dry seed-bed following a dry summer is favorable to flag smut, since spores and seed germinate together when the rain comes. On the other hand, if the soil is moist and has been so for some weeks, most of the flag-smut spores appear to have lost their effective power. These conclusions were supported by results in the general crop on the farm, and these views so strongly confirm those of the farmers that they practically amount to proof.

Conditions occurring in a particular Crop.—In the north and north-eastern districts of Victoria the flag smut was very prevalent during 1906, and was largely responsible, together with Take-all (*Ophiobolus graminis*), for the falling-off in the promised yield of many of the wheat crops. The conditions under which it occurred were very closely followed, and the particulars regarding it will be given for one district as a fair sample of the whole. In a 50-acre paddock near Wilby the Purple Straw Wheat was badly affected with flag smut, so much so that what promised to be a 20 to 24-bushel crop only turned out 8 bushels per acre. When inspected in the middle of November the general impression was that of a fine crop, but for the numerous plants scattered through it without ears, owing to flag smut. The conditions under which the crop was grown and all the defects conducted with its cultivation

were carefully recorded by the farmer, so that they are given here in connexion with the appearance of the smut. The soil is a rich alluvial red loam, with a sub-soil of clay at an average depth of 3 inches, and holding the moisture well. On analysis it was found that lime was very deficient.

The land is level, low-lying, but not swampy by any means, and has hitherto generally yielded splendid crops. The seed obtained from perfectly new land was carefully graded, dressed with bluestone at the rate of 4 lbs. to 50 gallons of water, and drilled in on 28th April. This was a very dry month, only .25 inches of rain having fallen, although the preceding month was very wet, having 5.55 inches. It was sown at the rate of 45 lbs. per acre, and Florida superphosphate along with it at the rate of 75 lbs. per acre. The flag smut was first observed in this paddock in 1903, the year after the dry season of 1902, and it was estimated that the loss due to it was about 8 bushels per acre. The wheat was followed by Algerian oats in 1904, with nitro-super. as manure. Then bare fallow during 1905, being ploughed in August, disced in November, and scarified about the middle of April. The ploughing was 3 to 4 inches deep. Up till about the beginning of October, 1906, the crop looked perfectly healthy and fresh, and then signs of disease began to appear. All through the crop the smutted plants were found generally destitute of ears, alongside of strong vigorous plants just coming into ear. To give an idea of the state of the crop, on 16th November a square yard of the average crop was measured off and the wheat plants grown on it carefully pulled. There were 144 smutted straws producing no grain, and 62 clean straws with healthy ears, or 70 per cent. affected with flag smut (Plate VII.).

The average rainfall is about 18 inches, but this was much exceeded in 1906, and distributed as follows :—

	Inches.		Inches.
January	.0	July	1.96
February	.16	August	2.28
March	5.55	September	2.76
April	.25	October	1.87
May	2.74	November	2.24
June	2.83	December	2.63
Total ..		.. .. 25.27 inches.	

After the very definite results obtained from sowing on a dry and a wet seedbed, as regards the appearance of flag smut, it seemed rather contradictory that the heavy rain preceding the sowing of the crop in 1906 should not have tended to reduce the amount of smut rather than increase it. But, as the farmer informed me that the cattle had the run of the whole paddock, both before and after the heavy rain in March, it is evident how the paddock was freshly infected with smut spores in the most suitable condition for germination. Laboratory experiments conducted in pots showed that with wheaten hay affected with flag smut fed to horses, the resulting manure was capable of infecting seed sown in the ground, and the farmer's cattle in this case were fed on such diseased hay straw.

During 1908 the flag smut was not so bad in this particular locality. On counting the smutted plants in a row 10 chains long it was found that there were about two diseased straws to every square yard, and the yield was 13 bushels per acre. At Dookie and Longerenong there were evidences of it being in the soil, but not widely distributed. At Dookie there were ten plots of 1 acre each on which selected wheats were sown. The seed was treated with bluestone, and the varieties were as follows :—Yandilla King, Marshall's No. 3, Australian Talavera, College Purple Straw, Dart's Imperial, Jumbuck,

C. C. Brittlebank, Phot. Nat. Size.

A—FLAG SMUT. B, C—LOOSE SMUT OF WHEAT.

(*Urocystis Tritici and Ustilago Tritici.*)

Jade, Comeback, Federation, and Bunyip. There was a little flag smut in each plot, but it was confined to a few plants, and the yield in no case was seriously affected.

At Longerenong there were also ten plots of selected wheats of 1 acre each. The flag smut was not so much in evidence, but there was a little of it in the four varieties—Australian Talavera, Dart's Imperial, Jade, and Federation.

Nature of Fungus causing Disease.

The flag smut of wheat belongs to the genus known as *Urocystis*, because the spores are provided with bladder-like appendages which in this case completely envelop them, and thus act as a protective covering. The spores are produced in long streaks on the flag, which soon curls up and withers, and thus the smutted portions of the plant become mixed with the soil under favorable conditions for the spores attacking the succeeding crop of wheat. As will be shown afterwards, they infect the plant at the seedling stage, or when the young shoots are formed, and generally destroy the entire stool, although sometimes a few ears may come to perfection beside those stalks which have withered and died. The dissemination of the spores is well provided for in nature by mixing with the soil, and the withered shreds and patches being blown about by the wind. Men and animals are also unconscious agents, not only in transporting the smutted earth from one field to another, but the agricultural implements may also carry it to otherwise clean fields. It can also be readily distributed by means of chaff and horse or cattle droppings. On examining 42 commercial samples of wheaten chaff from various parts of the State, only one was found free from the spores of this smut, and some of them were exceedingly bad with it. The disease was exceedingly bad in two cases, very bad in seven, bad in ten, common in thirteen, slight in eight, and very slight in one. Owing to the nature of the disease, the microscopical examination of chaff samples furnishes a very accurate guide as to the presence or absence of the disease in any particular district.

Geographical Distribution.

Although an allied species of smut is well known on rye in both Europe and America, the species on wheat is unknown there. It was first found in Australia, and since then it has been met with in India and Japan, and that is the extent of its distribution as known at present.

It is very widely distributed in South Australia, where wheat has been so long and so extensively grown, and in Victoria it is now more or less prevalent in the northern areas. In New South Wales it is probably more generally distributed than it is supposed to be, and in Queensland it has only been recently discovered.

Once this disease has gained a footing in a district there is every likelihood of it spreading if not kept in check, for it can be carried about by the farm implements and in the soil from diseased fields, and even in the manure from horses and cattle fed on the diseased hay.

Germination.

The germination of this smut was specially studied, because the spores on diseased straw in the soil, as well as those on the grain, were capable of infecting the young seedling. It has been tested for a period extending over three years, with spores of various ages, and at different seasons, in order to determine the period of its greatest activity. The most luxuriant germination was obtained about the beginning of April (autumn), and it is during the autumn months that the wheat is generally sown. The results of various germination tests will now be given. Spores were taken from the wheat-plant

immediately after maturity and placed directly in water on a slide, but they did not germinate. With material, however, about a month old, and kept seven days on soil, a small proportion of the spores germinated in water after 24 hours. There was considerable variety, but it consisted generally of a promycelium 1–6 celled, bearing at its apex 2–6 conidia. The promycelium reached a length of 66 μ and a breadth of 3–5 μ. The conidia at the apex were usually of unequal length, and they might either be unicellular with protoplasmic contents throughout, or 2–3 celled and only partially filled with dense protoplasm. At first they were close together, but gradually diverged and stood out as finger-like processes. In some cases they grew out into long slender filaments, reaching a length of 76 μ.

Spores were finally taken from wheat of last season and floated on tap water in a watch-glass in April. In about four days 40 per cent. had germinated, showing various stages of development. The longer or shorter promycelium was generally unicellular, but sometimes septate, and there might be only one germinal tube from a cluster of spores or occasionally two, and in one case each of the four spores in a ball germinated, producing conidia. The conidia were generally 3–4, at first unicellular and cylindrical, but afterwards becoming at least 1–2 septate. The earlier stages of germination show the conidia close together and relatively short, then they diverge and grow unequally. In some cases, one of the three or four may receive all the protoplasm and grow out as an elongated slender curved filament, in others, all the conidia may elongate and form variously curved and spreading filaments. The behaviour of these conidia, even in water, indicates how their germ-tubes may reach the host-plant, by growing stolon-like in the soil and penetrating a suitable host, if they reach it at the proper stage (Plate V., C.)

The conidia are formed by the splitting up of the promycelium at the apex into several branches, which are direct prolongations of it, like the fingers on the palm of the hand, although not all in the same plane. The conidia do not become detached, as a rule, although I have occasionally seen a few separate, truncate at the base and producing a slender germ-tube at the apex.

The Flag smut of wheat is closely allied to the stem smut of rye, and the germination of the latter is given here for comparison. Since Rye smut does not occur in Australia, specimens were collected by P. Sydow in the neighbourhood of Berlin on 21st July, 1907, and forwarded to me. The spores were placed on a slide with tap water added on 13th September, or 54 days after being gathered, and kept under a bell-jar. On the second day they showed signs of germination, and on the third day they were germinating freely and producing conidia at the apex of the germinal tube. The germinal tube varied considerably in length, sometimes reaching 100 μ or more, and at first was filled with protoplasmic contents. At the apex, a whorl of 2–6 cylindrical conidia were given off, generally 3–4. The germinal tube or promycelium is finally 4–5 septate and the contents in the lower portion of the tube are transferred to the upper. The apical conidia are very variable in size and shape. They are generally elongated, cylindrical, and either straight or slightly curved. Sometimes they may become prolonged at the apex while still attached, into a tapering filament, reaching a length of 50 μ or more.

The germination of stem smut of Rye has also been studied by Kuehn, Wolff, and Brefeld.

According to Kuehn[1] the fertile spores readily germinate in water and produce a longer or shorter unicellular germinal tube, which bears at its apex a whorl, consisting of two to six cylindrical conidia. They sometimes unite in pairs as in *Tilletia*, by means of a transverse bridge towards their upper ends, and often germinate while still attached by putting forth a slender germ-tube.

G. H. Robinson, Phot.

PRODUCE OF ONE SQUARE YARD
WITH FLAG SMUT.

Brefeld[5] also germinated the spores in water, and considers the whorl at the apex of the promycelium as branches, since they never become detached. In a nutritive solution it was the same, only the whorl of branches grew out and branched more freely. These cylindrical bodies at the apex of the promycelium behave like conidia, by putting forth a longer or shorter germ-tube, and there is no evident reason why they should not be regarded as such.

The conidia are said to give off lateral germ-tubes, and Wolff[1] gives a figure of one of the conidia producing a lateral germ-tube at its base. I have examined thousands of germinating conidia, and while the germ-tubes growing out at the tip may curve laterally, or even backwards, none were produced elsewhere than at the free end of the conidia.

Duration of Germinating Power.

These spores are well protected by their layer of sterile cells, and are well adapted from their structure to retain their vitality for some time. How long they retain their infective power, both in the soil and out of it, has not yet been definitely settled. In considering measures for dealing with the disease it is important to know how long this period lasts, for in a rotation of crops which is the most likely means of coping with it, it is necessary to know, if possible, how long the wheat crop has to be discontinued before it will be safe to sow it again. Experiments are being conducted to settle this point. A portion of a paddock, the soil of which is known to be badly infested with the smut, has been fenced off, and wheat will be continuously grown in certain parts of it to see how long, under ordinary cultivation and conditions, there is danger of infection, when every precaution is taken to prevent re-infection. Already pot experiments have been carried out, in which it was shown that seed dusted with spores from the crop immediately preceding was infected, while seed dusted with spores from the crop previous to that was not infected. But they are not sufficiently decisive and extensive enough to allow definite conclusions to be drawn from them.

Mode of Infection.

Since the host-plant is generally destroyed by this smut before the flowering stage is reached, infection through the flower is excluded, but experiments were carried out to test if it occurred in the seedling stage or later on. Seed wheat was obtained from a district in which this smut did not occur, and planted in pots containing ordinary garden soil. There were three pots—one used as a check in which the seed was uninfected, a second in which the seed was dusted with plenty of spores, and a third in which the spores were dusted over the plants when about 6 inches high. The result was that the smut developed only where the seed was dusted with spores, showing that it is probably the young seedling which is attacked, and that there is no infection when the plant is above ground. The experiment of dusting the seed with spores was repeated with a similar result, and when in another experiment the young plants about 3 inches high were also dusted with spores and kept moist by being covered with a bell-jar, there was no infection. In another experiment, affected straw from the previous season's crop was added to the soil, and the clean grain sown along with it. In about ten days after sowing the mycelium was obtained in the young leaf, and in 40 days after sowing the first production of new spores was observed. These conditions would be very similar to those occurring in the field, only there the diseased straw would be more in patches and not likely to be so generally distributed. In this experiment 18 plants out of 35 were diseased, or a percentage of 51.

The ordinary marketable chaff was also chosen, on which spores of the smut had been found, and a small handful was added to the soil of a pot, and the clean grain grown amongst it. Care was taken that there was no grains among the chaff which might possibly be affected independently, and in 40 days it was found that about 12 per cent. of the plants had become infected.

Finally, manure was added to the soil from horses which had been fed on diseased hay, and a small percentage of the plants was affected.

The following Table gives details of the experiments :—

Pot Experiments with Flag Smut, 1906–7.

No.	Date sown.	Grains sown.	Method of Infection.	No. plants germinated.	No. diseased	Remarks.
1A	13.11.06	100	Seed just germinated, then dusted with spores and sown	78	7	
1	22.11.06	50	Seed dusted with spores of 1906 crop	50	1	Plants died very rapidly, some probably diseased
2	27.11.06	50	Seed dusted with spores of 1905 crop	48	..	
3	29.11.06	50	Chaff sample badly smutted placed in soil and grain sown	42	6	All dead, 31.1.07; probably more than six diseased
4	30.11.06	50	Smutted straw of 1906 crop put in pot, 22.11.06; grain sown, 30.11.06	41	12	
5	6.12.06	50	Diseased hay fed to horse, manure put in pot and grain sown	42	1	All dead, 10.3.07
6	9.1.07	50	Diseased straw of 1906 crop put in pot, 22.11.06; grain sown, 9.1.07	35	18	Plants began to die rapidly about end of March
7	9.1.07	50	Diseased straw of 1906 crop kept in laboratory till date of sowing and then added to pot	18	1	All died very rapidly
8	9.1.07	50	Same as 5, manure in pot since 6.12.06; sown, 9.1.07	31	..	Died very rapidly
9	10.1.07	50	Same as 5, but manure left in box, only added to pot when seed sown	42	1	
10	26.2.07	50	Straw from 1906 crop kept on soil till date of sowing and then mixed with soil in pot	19	1	Soon died off

Control plots in every case free from disease.

These experiments prove conclusively that not only does infection occur in the seedling stage, or at least before the young plant has reached the surface, and when the spores adhere to the grain, but also when the spores are distributed through the soil on stubble or in the manure from horses fed on diseased hay. The failure of the different treatments, such as formalin, bluestone, and hot water, to prevent the occurrence of the smut, when the seed thus disinfected was sown in the soil containing the spores, also proves

that infection may arise from the soil, as well as from spores sown with the seed. By treating the seed dusted with spores with hot water, for instance, the development of Flag smut has been prevented, and the artificially infected grains produced healthy plants, but then the seed was sown in soil free from it. It was at first difficult to understand how the spores were able to infect the young seedling when they were not in contact with the grain, or had their germinating power destroyed by various re-agents. But, since the spores are capable of germinating in the soil and producing their elongated conidia, these conidia can in turn put forth a long tapering germ-tube, which may eventually reach the young plantlet as it emerges from the seed, or the young shoots formed beneath the surface.

Experiments in the infection of wheat with the spores of *Urocystis tritici* have also been carried out by Hori[1] in Japan. The spores were mixed with the moistened grains before sowing, and as the result of two years' experiments, while the uninfected seed produced clean plants, the infected seed produced both smutted and healthy plants in the ratio of 3 : 2. The conclusion come to is as follows :—" These two years' experiments decidedly proved that the smut is produced by the spores of *Urocystis occulta* [*U. tritici*] adhering to the seed coat, whither they have been carried by careless thrashing. But it may be possible, to some extent, that the matured spores, being easily scattered by winds, could also reach the inner side of the flowers, and this may be kept until thrashing time." The same investigator[1] also states that during a period of five years he tried many experiments to test whether spores in the soil infect the host. No details are given, only the general results. " After thoroughly mixing the spores with the soil, seeds of the wheat were sown in different intervals, partly on the same day, partly after five and ten days. But the results were always negative, and no difference with the control plants was noticed." In our experiments, as already shown, when diseased straw was mixed with the soil in pots, there was invariably a crop of more or less infected plants, while the control plants were clean. And not only so, but in one case at least the infection was much more virulent from diseased straw in the soil than from dusting the spores on the seed. It may be that sufficient moisture is necessary to decompose the straw, or at least to scatter the spores before they can produce their full effects, and in the pot experiments the plants were always well and regularly watered.

The conclusions to be drawn from our experiments as regards infection are—

1. Plants may be infected by coating the seed with spores.
2. Plants are liable to infection if seed is sown in soil containing diseased straw of the previous crop.
3. Plants may become infected if sown on soil containing manure from horses or cattle fed on diseased hay.

But a fresh light has been thrown on the infection of rye, and the same probably applies to wheat. By the experiments of Hecke, already recorded in Chapter VI., it was there shown that the spore has not only the one chance of infecting the primary or terminal bud, but also the numerous chances of infecting the lateral buds produced beneath the surface of the soil and growing out into fresh stalks. There is not only seedling infection, but shoot infection, and it is decidedly to the advantage of the parasite to multiply the points of attack as much as possible. This will explain how in an infected soil the seed may be quite free from spores and disinfected, while the young shoots are infected by the spores already in the soil.

Infection and Treatment.

The mode of infection has to be understood before methods of treatment can be intelligently applied, and this is particularly the case in dealing with Flag smut, which may either arise from the soil or the seed. A series of experiments were therefore carried out at Burnley Horticultural Gardens this season (1909) in order to test the effects of various modes of infecting the seed and of different kinds of treatment, both before and after infection. There were ten small plots altogether, each sown with 25 grains of the Federation variety of wheat, on 30th June, 1909, and three of these were used as a check or control plants to compare with the others. Both spores and diseased straw were used for purposes of infection. The wheat was thoroughly damped and rolled in the spores, while the diseased straw was chaffed up into small pieces and placed around the seed when planted. The following table gives the relative results :—

Plot.	Grains sown.	Grains germinated.	Mode of Infection and Treatment of Seed.	Results.
47	25	19	.. ..	Clean
48	25	24	Dusted with spores	20 plants flag-smutted = 83 per cent.
49	25	25	Dusted with spores and blue-stoned	Clean
50	25	18	Dusted with spores and diseased straw added	15 plants flag-smutted = 83 per cent.
51	25	21	Diseased straw only added ..	11 plants flag-smutted = 52 per cent.
52	25	24	Bluestoned and diseased straw added	7 plants flag-smutted = 29 per cent.
53	25	25	Bluestoned and spores added ..	Clean
54	25	25	.. ..	Clean
55	25	24	.. ..	Clean
62	25	25	Treated with corrosive sublimate and diseased straw added	11 plants flag-smutted = 44 per cent.

Without laying too much stress on details, on account of the small size of the plots, it is evident that infection may be produced either from spores adhering to the seed or by means of diseased straw occurring in the soil where the seed is sown. The addition of diseased straw to grain already dusted with spores did not increase the virulence of infection.

Again, when the seed was infected with spores and afterwards treated with bluestone, the germinating power of the spores was destroyed, as the resulting plants were all clean, and when the grain was treated with bluestone before the addition of the spores no infection occurred.

If, however, the grain was treated with bluestone and diseased straw added, there was infection to the extent of 29 per cent. This could easily be accounted for from the young shoots being attacked which had no protective coating of bluestone. Even when the grain was treated with corrosive sublimate and diseased straw added there was still a large amount of infection.

Thus, the general results already obtained are corroborated, that if the spores are only on the grain and no Flag smut in the soil, treatment with bluestone is a preventive ; but if the diseased straw is already in the soil from a previous crop, neither treatment of the seed with bluestone nor corrosive sublimate is effective.

Infection by diseased straw alone, as compared with spores on the grain, was also tested in 1908. Two hundred grains of Federation were sown in four divisions, the first having diseased straw added, and the other three had the seed dusted with spores. The results were practically the same in each case, as there were respectively 11, 13, 14, and 12 per cent. of Flag smut.

There is a discrepancy here between the results obtained by experiments in pots and in the field, for in the pots the diseased straw produced much more severe infection than the spores. This may be due to the fact that the regular watering of the pots would have a tendency to remove the spores adherent to the grain, while in the case of diseased straw it would tend to be absorbed, and leave the spores undisturbed.

Infection of Wheat and Rye.

The Flag smut was first found on wheat in Australia and was determined by Wolff in 1873 as being the same as that so abundant on rye elsewhere, and named *Urocystis occulta*. Then Koernicke in 1877 considered the form on wheat to be a new species, basing his determination on morphological characters alone, and named it *Urocystis tritici*. If the same species of smut occurred on both plants, then they ought to be mutually infective, the spores from rye infecting the wheat, and the spores from wheat infecting the rye, and infection experiments alone could settle it.

The first experiment was carried out in pots containing ordinary garden soil, and wheat and rye were cross-infected. There were six pots, and wheat and rye were sown in them on 11th October, 1907. The ordinary seed of wheat and rye was used as a check. Then seed wheat infected with the spores of Flag smut from wheat collected on 28th September, and another lot with those from rye collected on 21st July. Finally rye seed was infected with the spores of Rye smut, and another portion with those from wheat.

The first outbreak was in the rye infected with Rye smut, 40 days after sowing, and about a week afterwards the wheat infected with the Flag smut of wheat showed the disease. The rye germinated about two days before the wheat. Although several plants germinated, only one each of rye and wheat showed distinct traces of the disease, and they were each infected with their own particular smut. These pot-experiments are very useful for giving indications of what may happen in the field, and they often show what to avoid, as well as what to follow, upon a large scale. Another experiment was planned, conducted in my own garden, in which there were six plots, with 20 grains each, but otherwise similar to the first ; the same smut of wheat and rye being used for infection as before. They were sown on 23rd May, 1908, and on the 28th October three wheat plants out of twenty were found badly infected with Flag smut, the infection having been brought about by the spores of wheat Flag smut.

The plots were finally examined at the end of the year, but there was no further development of disease. Although in these experiments there was no disease in the rye, it was not owing to the spores being non-germinable, for when placed on a slide in tap water and kept under a bell-jar they germinated freely in three days. On 12th August, 1908, I duplicated the plots, in order to see what effect very late sowing might have upon the result. The same smut of wheat and rye was used for infection. The late-sown rye grew much better than the late-sown wheat, the latter in fact, turning out a comparative failure. In this experiment two plants of rye were found on 6th January, 1909, to be badly infected with their own smut, but none appeared in the wheat plots, neither from infection with Flag smut of wheat nor with Rye smut.

A final experiment was undertaken at Burnley Horticultural Gardens, in which 200 grains of Federation wheat were inoculated with the spores of Flag smut derived from a crop of wheat grown in the north of Victoria the previous season, and 200 grains of rye inoculated with the same smut. Clean seed of both was sown alongside, the date being 28th June, 1908. The object of this test was simply to see if wheat and rye could be infected by the same smut. The results were taken on 29th December, and, while the wheat was diseased, the rye was absolutely clean. There were 190 plants of wheat altogether, 21 of which were affected with Flag smut, and 169 clean, so that 11 per cent. were diseased.

The diseased plants bore 85 ears, and on counting the ears of 21 healthy plants of the same variety growing alongside there were 165, or nearly double the number. The photograph of the two bundles of wheat, each representing the produce of 21 plants, shows the difference in yield of the healthy and diseased. *A* represents the growth of the healthy plants, and *B* of the diseased, and the proportion of ears in *A* is nearly double that of *B*, indicating that the number of ears on each plant affected with the Flag smut fungus would be reduced, on an average, about one-half (Fig. 12.)

In Fig. 13 is shown the grain from the healthy and diseased plants, and the yield from the former is fully three times that of the latter.

Fig. 12.—Clean and Flagsmutted Wheat.
A.—21 healthy plants ; B.—21 diseased plants.

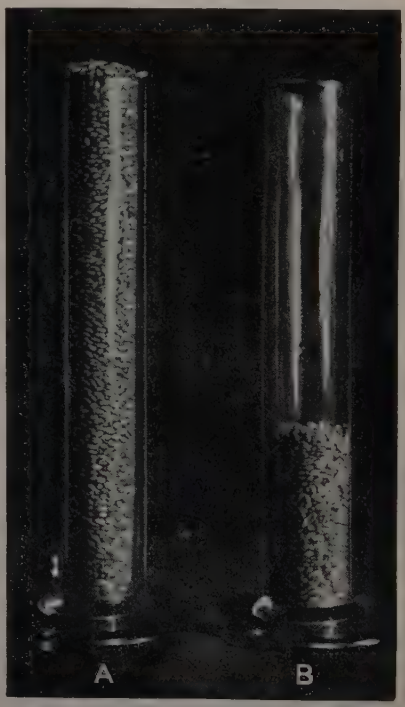


Fig. 13.—Grain from healthy and diseased plants.
A.—21 healthy plants yielding about 8 oz. of grain ; B.—21 diseased plants yielding exactly 2½ oz.

The main conclusion to be drawn from these experiments is, that the Flag smut of wheat and rye are not mutually infective, and therefore the name given to Flag smut of wheat by Koernicke in 1877, who received specimens from R. Schomburgk in South Australia, should be retained, viz., *Urocystis tritici.*

Preventive Measures.

From the very nature of this disease it is difficult to cope with, since it not only infects the young seedling when the spores are attached to the grain, but they may also be in the soil and carried by various agencies from one paddock to another. Hence the soil would require to be disinfected in order to render any treatment of the seed efficacious, and that does not seem practicable at present. The effect of various manures has been tried, including the application of ground quick-lime with the seed, and two of lime to one of sulphur in combination, but the results were not promising. It is believed that a proper system of rotation will be one way of solving the difficulty, and experiments are now being carried out in that direction.

There are, however, certain recommendations that may be made from our present knowledge of the fungus, which will tend at least to reduce the ravages of the disease—

1. *Wheat after wheat should be avoided.*—It is not only bad farming practice to grow wheat after wheat, but it is a sure means of perpetuating the fungus in the soil, since a fresh crop of the fungus will be produced year after year if the conditions are favorable. If we wish to starve out the fungus we must sow some other crop on which it does not live, and it is well known that oats are exempt from this particular smut.

2. *Early fallow, with thorough working.*—The practice is now becoming general of taking off only one *wheat* crop every three years. The stubble is allowed to stand after harvest, and any grass which springs up serves as pasture. Then, in the second winter or spring after the wheat crop the land is fallowed, and in the following autumn the wheat is again sown. This is the ordinary three years' rotation of *grass*, *fallow*, and *crop*, and it would be well occasionally to replace wheat with oats. The thorough working of the land after rain through the spring and summer is as important as the fallowing. By working the land under these conditions air is admitted and moisture is conserved, and this favours the germination of the spores, and, in the absence of suitable plants to grow upon, they soon perish. On the other hand, dry-worked land is specially favorable to the disease, for this simply encourages the spread of the spores, and preserves them in a dormant state, so that they are ready to germinate along with the wheat plant.

3. *Burning the stubble.*—This is not so commonly practised as it used to be, since the value of the straw is now recognised. But badly affected paddocks should be burnt off, in order to destroy the spores of the fungus and check the spread of the disease, and this must be done with reference to the object in view. If the patches are too bare to burn where the Flag smut has been then the harrows should be run over the stubble and the straw will be drawn to such patches and a profitable burn-off effected.

4. *Selection and breeding of resistant varieties.*—Among the different varieties grown there may be some which more successfully resist the Flag smut than others when grown under similar conditions, or there may be perfectly clean individual plants among the diseased, and such might be selected for further trial. Early varieties are said to be most susceptible,

and that is probably because they are more likely to be infected by the spores at the proper time for germination. Late wheats do not suit our conditions; so that the selection should be made from early maturing varieties.

Now that a certain measure of success has been gained in securing rust and bunt-resisting wheats, similar methods may be adopted with regard to Flag smut, and a smut-free late wheat, crossed with a susceptible early variety, might lead to earliness combined with smut-resistance.

Summary.

Flag smut of wheat does not infect rye, and rye smut does not infect wheat; so the form occurring on wheat is a distinct biological species, and is, therefore, named *Urocystis tritici*, Koern.

Infection occurs in the seedling stage, also when the young shoots are being formed, but not when the plant is above ground, and this infection may arise either from spores adhering to the surface of the grain or from diseased straw or fragments of flag in the soil. The spores may persist and retain their vitality on wheaten chaff, and soil containing manure from horses and cattle fed on diseased hay is capable of infecting the wheat plant.

The adherence of the smutted soil to the feet of men and animals may cause it to be transported from one place to another, and agricultural implements also scatter and carry it.

Since this smut is only known to attack wheat, a change of crop will evidently tend to starve it out; but as it is not known how long the spores retain their germinating power, the nature and extent of the rotation cannot yet be determined.

CHAPTER XV.

Loose Smut of Oats.

(*Ustilago avenae* (Pers.), Jens.)

This is a disease which is known wherever oats are cultivated, and caused enormous losses before methods of prevention were discovered. The spores are produced exclusively in the spikelets, and every part of the inflorescence may be attacked, even the glumes and the awn (Plates VIII. and IX). The ovaries are filled with the spores, and the ovary wall remains as a delicate wall around them. The diseased ears may be seen emerging from their enveloping leaf-sheaths, and when exposed the membrane is soon ruptured, and the powdery spores are blown about by the wind, or washed away by the rain, leaving only the bare axis of the inflorescence with the ragged remains of the envelopes of the flowers. Generally, all the shoots of a plant and all the grains of the ear are attacked, but in some cases the upper spikelets may be free. In a partially-smutted ear, although the tip may be sound, the base is always affected. In no case has the upper portion of the inflorescence been found diseased, while the lower was sound, thus showing that infection proceeds from below upwards, and that when the inflorescence began to elongate, the smut had not reached the uppermost point of the panicle.

The spores are scattered before harvest-time, even before all the oat plants have ceased flowering, and thus many of the smut spores are enclosed by the scales, which gradually envelop the ripening grain, or they may fall on the ground, where they will be ready to germinate under the same conditions which favour the sprouting of the seed oats.

Germination.

This has been reported and illustrated in comparatively recent times by Brefeld[1] in 1883, by Kellerman and Swingle[3] in 1890, and by Herzberg[1] in 1895. Fresh material was gathered in November, 1906, and germinated during the same month. When placed in water the spores begin to germinate usually in six to eight hours, and it is more rapid in summer than in winter, and with fresh spores rather than with those kept for several months. A germinal tube or promycelium, occasionally two, is produced by an out-growth of the endospore bursting through the exospore, and the protoplasm contained in the spore passes into the tube. The rupture is sometimes so pronounced that the projecting portions of the exospore are seen along each side of the base of the tube. Then it becomes divided by three to four transverse partitions into equal compartments. From each of these compartments, as a rule, little off-shoots or buds arise, generally near the septa, and almost always one is produced at the apex. These buds constitute the promycelial spores or conidia, and they become elongated and ovate, and then fall away. The protoplasm in each segment is used up in the formation of conidia, and if this is exhausted then no more are formed. But sometimes the protoplasm is not all used up, and the primary conidium, instead of falling away, remains attached, and gives off at its free end a small bud, which gradually becomes a secondary conidium, although it does not attain the size of the parent.

The conidia when detached undergo further changes in water. They may either put forth a very narrow-pointed germ-tube, into which the protoplasmic contents pass, or two adjacent conidia may become connected by a transverse branch, and the contents pass from the one into the other. Then

the one with protoplasmic contents puts forth a germ-tube, or it may swell out at the end and form another conidium. Thus fusion of the conidia occurs where a number of them are aggregated together, and even more than two may in this way be united.

This is the typical mode of development, the spore producing a germinal tube or promycelium, from which conidia are budded off, but there are various departures from this. Under certain circumstances, according to Kuehn, the promycelium may not develop conidia, but becomes an ordinary hypha and penetrates the tissues of the host-plant by its pointed extremity. Again, various fusions may take place by means of a tube from one segment to another of the same promycelium, or the promycelia from different spores may unite in a variety of ways by means of branches. Thus, the upper segment may become connected with the lower segment of the same promycelium by means of a curved tube, or two succeeding segments may become united by what Brefeld calls a buckle-joint or knee-joint. This is very common with spores germinated in both water and nutritive solutions, and consists of the unequal growth of one side of the promycelium at the level of a septum. As this protuberance grows the promycelium itself becomes bent at an angle.

So far the behaviour of spores in water has been shown, but when placed in a nutritive solution, such as hay infusion, there is a difference, as Brefeld has pointed out. In the first place, they germinate quicker, as might be anticipated, and the promycelia and conidia are larger. Then the various fusions do not occur, but the most important difference is that the detached conidia multiply themselves by budding after the manner of yeast and form what are known as sprouting conidia. By keeping up a supply of the nutrient fluid, Brefeld maintained this process of budding for more than a year, and, whenever this was exhausted, the budding ceased. The sprouting conidia retain their vitality for about two months if kept moist, but when allowed to dry there was no germination after the sixth week. It becomes a question of great practical interest how long the various reproductive bodies retain their germinating power and under different conditions of moisture. While the sprouting conidia only retained this power for about six weeks when kept dry, Brefeld found that the spores germinated as freely at the end of two years as when fresh. Another observer, Von Liebenberg[1] germinated the spores at the end of seven and a-half years, so that the time limit of germination may exceed that considerably.

Infection.

Infection by this smut has been specially studied by Brefeld,[1] and a description of it will give a clear idea as to how this happens in smuts of this type. The spores are produced exclusively in the spikelets. It had already been shown by Wolff[1] and Kuehn[1] that infection takes place only in the seedling stage, and Brefeld followed the mycelium in the growing plant until it reached the ovary of the flower and formed its spores.

He brought about infection not directly with the spores, but with pure cultures of the "yeast-spores," or sprouting conidia, derived from the budding conidia grown in a nutritive solution. The young seedlings specially grown were sprayed by means of an atomizer, with the "yeast-spores" mixed up in water, and after a short time were planted out. According to the stage of growth at which the seedlings were infected, there was a definite percentage affected with the disease. In the earliest stage of the seedling, while still in the bud, 17 to 20 per cent. were diseased; when about 1 cm. long, there were 7 to 10 per cent. diseased; when 2 cm. long, and still enclosed in the sheathing leaf, there were only 2 per cent. diseased; while in older seedlings there was

G. H. Robinson, Phot. Nat. Size.

LOOSE SMUT OF OAT

(Ustilago Avenae.)

practically no infection—0 to 1 per cent. diseased. These experiments conclusively prove that the younger the seedling the more susceptible it is to infection.

The course of the infection was closely followed. The germ-tube penetrated the cuticle and grew obliquely through the cells. In the earliest stages of the seedling the hyphae were numerous and distinct; but as the tissues lengthened and strengthened it was more difficult to trace the mycelium. In the fully-formed plant the mycelium could only be detected in the tissue of the nodes, in a more or less ruptured condition. The fungus is unable to keep up with the rapid longitudinal growth of the plant, and its mycelium is torn up into fragments, so that it becomes isolated and does not reach a suitable spot for the production of spores. In the rapid elongation of the internodes the oat therefore exercises a kind of check upon the parasite, but, on the other hand, if the mycelium has once reached the growing point then it is always present there, and finally produces its spores. It is evident, therefore, that not every infection of the host-plant will necessarily attain to the production of spores, but only in those cases where the fungus has been able to reach the tissue of the growing point and continue to keep up with it until the flowering stage. This supplies an explanation of the fact that infection is much more successful in younger than in older seedlings, for in that case the mycelium can much more easily reach the growing apex and remain there than when the elongation of the internodes has taken place.

There are several conditions which render infection more or less certain, and also affect its virulence. If the "yeast-conidia" used for spraying the seedlings were cultivated in a solution obtained from fresh horse-dung, then there might be as much as 46 per cent. of diseased plants, and if the spores were cultivated for a number of generations the virulence decreased towards the end. Spores that have wintered in the soil will, under suitable conditions, germinate in the spring and form conidia; but whether these conidia will infect young plants directly or sprout in a yeast-like manner or die, will depend upon the weather, particularly in regard to the heat and the moisture. Since our sowing time is generally in the autumn and before the winter, the problem we have to solve is what happens to the spores in the soil during the summer, as, by the time winter is reached the spores have either germinated or have missed infecting the seedling stage.

This smut produces its spores in the ovary of the flower; then they are dispersed by the wind or rain, and some of them fall on the soil or are carried to healthy grain. Infection takes place when the seed begins to germinate, and the young mycelium grows along with the seedling, showing no external signs of its presence until the flowers are produced, when it again forms its spores in the ovary. Jensen[1] proved that oat smut will not infect wheat or barley, and that it is, therefore, biologically distinct from the smuts attacking either of these cereals.

Between the loose smut of wheat and of oats there are marked differences in the behaviour of the two. To begin with, the spores in the case of wheat only retain their germinating power for a few months, while in oats they have been germinated at the end of seven years.

Then again, on germination the wheat loose smut only produces a germ-tube, which may be variously branched, while in oats not only are conidia formed, but these in turn may give rise to sprouting conidia.

These differences are correlated with the mode of infection. In wheat it is flower infection, which must be done within a limited period, and after the manner of a pollen-grain, and in oats it is seedling infection, which may be prevented by treatment similar to that of stinking smut of wheat.

Treatment of Seed.

It is the seedling which is infected, and therefore the destruction of the spores on the seed will prevent the disease; but from the nature of the smut and the nature of the oat-grain itself, certain precautions must be taken in the treatment of the seed. Unlike the stinking smut, the spores of the loose smut are blown about by the wind before all the oat-plants have formed their seed. The consequence is that spores find their way between the scales, which ultimately firmly clasp the seed, and any solutions which merely wet the outside will not reach these enclosed spores. Hence, any treatment to be effectual must be sufficiently prolonged to allow the solution to reach the spores beneath the hull of the oat. Treatment with hot water is, therefore, very effective, and Close[1] has shown that sprinkling the seed with a 1 per cent. solution of formalin entirely prevents the disease. The drawback to the use of bluestone is that in order to reach the spores the seed must be dipped so long as to injure it.

C. C. Brittlebank, Phot.

Nat. Size.

LOOSE SMUT OF WILD OAT

(Ustilago Avenae.)

CHAPTER XVI.

Naked Smut of Barley.

(*Ustilago nuda* (Jens.) Kell. and Sw.)

It was first pointed out by Jensen[1] that there are two distinct kinds of smut on barley. The one completely destroys the ear, being at first enclosed in a thin silvery-looking membrane, which soon breaks, and the powdery spores are scattered by the wind as soon as mature. This is known as the Naked smut (Plate X.) in contradistinction to the other, which is called Covered smut, because the compact mass of spores is enclosed in the unbroken walls of the ovary, and remains intact for some time, even after harvest. The heads of barley with Naked smut resemble those of the wheat when affected with loose smut, and this resemblance extends even to the mode of infection, which in both cases occurs in the flowering stage.

Germination.

The germination of the spores of *U. nuda* and *U. tritici* is quite different from that of *U. avenae* and *U. hordei*. In the two latter, as has been shown, a promycelium is formed, giving rise to conidia, while in the two former a typical mycelium arises. The spore on germination produces a separate germinal tube, which continues to grow at the apex and forms lateral branches which in turn branch again, and so a spreading mycelium is developed without the formation of conidia. This important difference in the mode of germination led Herzberg[1] to propose a new genus—*Ustilagidium*—for the reception of these two species.

The germination of this species has been described by Kellerman and Swingle,[3] Brefeld,[4] and Herzberg,[1] among others. Spores obtained from barley grown at Myrniong in 1906 germinated freely in water and in a nutritive solution in May, 1907. When grown in water a straight septate germ-tube was first formed, the protoplasm of which was highly vacuolated, and at first divided into four cells by transverse septa, then branches were sparingly given off beneath the septa, sometimes at right angles, but generally at an acute angle. The germ-tube sometimes became attenuated towards the apex, and, although branches might be given off near the base, yet in no instance was a spore met with producing two independent germinal tubes.

In a nutritive solution the branching was much more copious. Brefeld[5] found that the filaments grew rapidly in various directions, and produced a branching system like the mycelium of the higher fungi. The ends of the filaments continued to grow in length, the contents passing from behind forward and formed very long tubes, which afterwards became septate. Their branches were produced below the septa, and continued the process until the central parts of the original mycelium were gradually drained of their contents and carried to the circumference of the filaments.

The spores do not long retain their germinating power, as it was found not to have lasted for a year, and this, along with the absence of conidia, would seem to indicate that the spore must germinate as quickly and directly as possible in order to penetrate the stigmas of the flowers that are in bloom.

Infection.

Brefeld[7] and Hecke[3] have both recently shown that infection takes place through the flower. It was found that when infection of seedlings was attempted only negative results were obtained, and in every case sound healthy

plants were produced. But when floral infection was carried out the results were the same as in the Loose smut of wheat, the mycelium remaining latent in the seed and developing spores when the young ovaries of the host-plant were formed.

From the nature of the flower of the barley and its being more firmly enclosed in the glumes than is the case in wheat, it was not so easy to carry out artificial infection and with the same certainty of results, but the experiments showed that infection of the flower is the main, if not the only mode. Hecke infected a number of the flowers of barley with smut spores when the ovaries were still undeveloped, and the stigmas were quite fresh. Then, when the fruit had normally ripened, and had been properly disinfected, it was placed under sterile conditions in a germinating chamber, in order to examine the embryo or young plant at different stages of development. If an embryo is examined just beginning its development, even at this young stage numerous hyphae are seen in a longitudinal section. In Fig. 6 a slightly more advanced embryo is shown, and the mycelium is copiously developed at the junction of the first leaf with the growing apex. (*v*). There can be no doubt that this is the mycelium of the smut produced by flower infection, since it is only found in infected seeds, and the subsequent infection of the seed during germination is completely excluded by treatment with a fungicide.

G. H. Robinson, Phot. Nat. Size.

NAKED SMUT OF BARLEY

(*Ustilago Nuda.*)

CHAPTER XVII.

Covered Smut of Barley.

(*Ustilago hordei* (Pers.) Kell. and Sw.)

This smut is not so readily observed as the Naked smut, and therefore it is sometimes said to be not so common, but as to relative prevalence it is found to be the more common of the two. At Dookie, where a number of varieties of barley are grown, it is much more general than the Naked smut, and it is a very marked feature of the skinless barleys. This wider distribution may be due to the compactness of this smut, which gives it exactly the same chance as Stinking smut of wheat, which is distributed in a wholesale manner in the form of smut-balls, and also to the fact that the floral infection necessary in the Naked smut will be more uncertain (Plate XI.).

The two species of smut found on cultivated barley (*U. hordei* and *U. nuda*) have only comparatively recently been separated, and they were formerly included under *U. segetum*. The differences between the two are very marked, independent of what is indicated by the common name. In the Naked smut the diseased ears are ultimately free from the leaf-sheath and fully exposed, while in the Covered smut the ears are more or less enclosed. The spores in the former are echinulate and powdery, and scattered by the wind at the flowering period, while in the latter they are smooth, slightly larger and compact in the mass, and remain intact till later harvest. In the Naked smut the spores in the mass have a decided greenish tinge, which is absent from the Covered smut. The germination, too, is very distinct. In the Naked smut only a germinal tube is formed, which elongates and branches and becomes a regular septate mycelium, but in the Covered smut conidia are produced. Lastly, the Naked smut has been proved to infect the flower and not the seedling and the Covered smut infects the seedling, as indicated by the certain treatment of the seed with bluestone solution. The differences between the two may be briefly summarized :—

Covered Smut.	*Naked Smut.*
Ears—More or less enclosed in leaf-sheath	Free from leaf-sheath.
Spores—Compact in mass, with greenish tinge, smooth, and remaining intact till after harvest	Powdery, echinulate, and scattered during flowering time.
Germination—Conidia produced ..	No conidia.
Infection—Seedling	Flower.

Germination,

The germination of the spores has been described by Kellerman and Swingle,[3] Brefeld[4] and Herzberg. Affected barley was obtained from the neighbourhood of Melbourne in November, 1906, and the spores germinated freely in water in December. Also from Port Fairy in January, 1907, and when tested in June the spores readily germinated. The promycelium was generally 3-septate, only one being formed from each spore, according to Herzberg, but I have found occasionally more than one. Promycelial spores were produced both laterally and terminally, and were generally attached by a slender sterigma, sometimes two being given off together, each with their own sterigma. The promycelium was sometimes branched, the branches becoming septate and giving off conidia, and knee-joints were very common,

as in other species. Along with the single promycelium arising from the spore, there might be given off at another part a large oval unicellular body behaving like a conidium. The conidia which are elongated ellipsoid, readily fall away when they multiply independently by budding.

In a hay infusion the promycelia branched copiously. Slender elongated branches were given off, and sometimes on a level with the septum where a knee-joint might have been, there were long jointed hyphae. Brefeld has shown that the conidia multiply in a yeast-like manner and form sprouting conidia, which continue to develop as long as nutritive material is supplied.

Infection.

This occurs, in all probability, in the seedling stage, as indicated by the certain treatment of the seed and the formation of sprouting conidia in order to tide the fungus over from one season to another. The spores are very commonly found on samples of barley, so that they must reach the sound grain during thrashing.

G. H. Robinson, Phot. Nat. Size.

COVERED SMUT OF BARLEY

(*Ustilago Hordei.*)

CHAPTER XVIII.

Head Smut of Maize.

(*Sorosporium reilianum* (Kuehn) McAlp.)

This is the only known smut of maize known at present in Australia, and it is spreading in districts where maize is largely grown. It attacks the cobs and tassels (Plates XII., XIII.), and is usually confined to them, but, in exceptional cases, a few patches of smut may appear on the upper leaves. The smut is enclosed at first in a pinkish membrane, which soon ruptures in order to allow the escape of the spores. It is distinguished from American Corn smut (*Ustilago zeae* (Beckm.) Unger.) by not enlarging the ears and forming large smut boils, by generally confining itself to the inflorescence and not attacking the leaves and stems, and by the larger and more finely echinulate spores. It was probably introduced here from America, although not a native of that country, for, as Clinton[4] says—"This is one of our most conspicuous but rather uncommon smuts. It has been introduced into this country, probably from Europe." This species was first named from a specimen on *Sorghum vulgare*, Pers., sent by Dr. Reil from Egypt, and it was afterwards found in Italy on the same host-plant. Its introduction into America was probably by means of this host-plant, and then it spread to maize, as it is found on both plants in the United States.

Germination.

The maize was taken from the field about the middle of March, just about two months before maturity, and the smutted cobs were still contained within their enveloping bracts. The smut spores were at once placed in tap water on a microscopic slip and placed under a bell-jar, and in 17 hours several had formed germinal tubes consisting of three to five cells, but usually four-celled, although none had formed conidia. On germination there is an evident rupture of the exospore, which is split into lobes where the germinal tube protrudes. In 21 hours conidia were formed, both terminally and laterally, and the terminal conidia are the first to be formed. In one which was specially observed the elongated terminal conidium was first formed, then one laterally from the top of the second cell from the base, and a third just beginning to be formed from the top of the basal cell on the opposite side. The contents of the germinal tube are highly vacuolated when producing the conidia, which are sometimes formed in pairs at the apex, and three lateral conidia are sometimes produced together. Occasionally the germinal tube may branch and the conidia may be borne direct or on elongated slender sterigmata. The conidia bud in a yeast-like manner, and these sprouting conidia again give rise to secondary conidia.

Brefeld[1] germinated the spores in a nutritive solution after being kept for about eight years, and the sprouting conidia retain their germinating power for several months, if kept dry.

Infection.

The mode of infection has not been determined, but, since according to Freeman and Umberger,[1] the formalin and hot-water treatment of the seed are ineffective, the probabilities are that it does not occur through the young seedling, as in the case of Bunt, but may be in the grain itself. These authors state that the only recommendation that can be made at present is to obtain

seed from districts where it is not known to occur. It is interesting to note that the "Milo" variety of Sorghum has not hitherto been attacked and appears to be immune.

American Corn Smut.

(*Ustilago zeae* (Beckm.) Unger.)

This smut, which occurs on all parts of the maize plant, has not been found in Australia, although there is another species met with which is confined to the ear, but since this species represents one of the typical modes of infection, it will be briefly discussed.

The spores have not been found to germinate in water, but very easily in a nutritive solution or on manured soil, producing the fusiform conidia. These do not directly infect the plant, but give rise to sprouting conidia, and very often they also put forth fungus filaments which reach the surface of the culture drop, and there develop quite a number of sprouting conidia in the air, similar to those produced in the fluid. These air conidia are easily scattered by the wind, and play an important part in spreading infection.

Since this smut occurs on all young and growing parts, most rarely on the roots and most frequently on the stems, leaves, cobs, and tassels, it is evident that we have not to do with a general infection of the plant, but with a local infection, each smut-boil representing a single infection. Brefeld[1] carried out a systematic series of infection experiments, infecting the various parts of the plant. He started with the young seedling, as in the case of the oats, but produced only a few diseased spots, and always in the neighbourhood of the collar or at the junction of root and stem, while all the other parts of the plant were unaffected. Then, in other parts he infected the leaves and the stem, the male and female flowers, and even the young ovaries of individual flowers, always with the same result. The infection was exclusively local, and it was only young and tender tissues which the germinating tube could penetrate. When the fungus filaments had reached maturity they broke up into spores in the usual way, with gelatinization of the membranes, and it was observed that from the period of infection until the spores were produced and scattered was about three weeks.

G. H. Robinson, Phot. ½ Nat. Size.

MAIZE COB WITH HEAD SMUT

(*Sorosporium Reilianum.*)

G. H. Robinson, Phot.

¾ Nat. Size.

MAIZE TASSEL WITH HEAD SMUT

(Sorosporium Reilianum.)

CHAPTER XIX.

General Treatment for Smuts.

It is only when the true nature and the life-history of the smuts are properly understood that intelligent measures can be devised for effectually coping with them, and the treatment will depend on the individual history of each particular species. But the general rule may be laid down that in every case clean seed should be used for sowing, for, as Bessey[1] emphatically points out, "It has been demonstrated over and over again that perfectly clean seed and clean ground will produce a clean crop. It is with smuts as with weeds of all sorts, if we have seeds we shall have weeds growing up as a result, but if we have no seeds there will be no weeds. So with smut. Clean seed upon a clean field will result in a clean crop."

Since it has been clearly shown that the smuts are reproduced from spores, it is evident that if the spores can be destroyed or their germination prevented, the smut itself will not appear, and it is on this principle that the direct treatment for smut is based. But this method is only practicable when the spores are so located that they can be easily reached as in the seed grain, and in other cases only indirect measures can be employed. In the bunt or stinking smut of wheat for instance, where the spores adhere to the grain and infection occurs in the young seedling, all that is necessary is to treat the grain with some substance which, while harmless to the grain, will destroy or prevent the germination of the spores.

Quite a number of substances have been used for this purpose, including corrosive sublimate, and found more or less effectual, but there are only two which are generally used by farmers in Australia on account of their ease of application and comparative cheapness, and that is, first, a solution of sulphate of copper or bluestone, and, second, formalin. All methods of seed treatment known depend for their success to a large extent on the precautions taken to prevent re-infection after dipping. Careless farmers put the pickled grain into smut-infested bags or omit to clean the drill. If the seed-box contains bunt balls or spores of other smuts the treated seed will be, in part at least, affected.

I adopt a very simple method in the treatment of the seed-wheat, the solution being contained in a wooden cask. The mouth of the bag which is immersed in the solution, and that is to contain the seed, is slightly folded over the edge of the cask and fastened there with a bag ring or hoop. The seed is then gently poured into the sack, so that all the unbroken smut-balls as well as wild oats and light seeds float on the surface and may be skimmed off. In the case of bluestone solution the time of immersion should never exceed one minute, as every grain is sure to be thoroughly wetted in that time. A supply of the same strength of bluestone solution is kept ready, in order to replenish the solution in the cask used for pickling, as required.

Bluestone Treatment.

This is the one most commonly used here, and consists in making a solution at the rate of 1 lb. of bluestone to 5 gallons of water, or a 2 per cent. solution. The seed is then placed in sacks and immersed in this solution until every individual grain is wetted, and that only takes about a minute, and should not exceed it. The constant shaking and stirring while being immersed should bring all bunt balls to the surface, and these should be skimmed off. The bag is then allowed to drain, and when dry the seed is ready for sowing.

It is to be noted that the solution of bluestone is always of the same strength as when first prepared, no matter how much of it has been used up in dipping or in coating the grain. It becomes, of course, reduced in quantity, and if exposed to the hot sun for several days, it would become more concentrated, but under ordinary circumstances the standard solution remains constant in its proportion of bluestone to water.

If more convenient the seed may be pickled on the barn floor by sprinkling the solution over it and thoroughly turning over the seed until all the grains are completely wetted.

The corrosive action of the bluestone on the grain is generally very injurious, and this can be largely prevented by the use of lime. It may be pointed out that the copper sulphate or bluestone is gradually decomposed by the lime, and acting chemically upon the soil renders certain substances available as plant food. The treated seed, while wet, may be sprinkled with air-slaked lime, but this interferes with its ready passage through the seed drill. As an alternative the treated seed may be transferred to lime-water. One pound of freshly-slaked lime in 8 gallons of water gives full strength after standing one hour, and traces of alum or sulphate of magnesia increase the solubility of the lime slightly. The grain is stirred in this solution for a few minutes, then dried preparatory to sowing. An objection to the lime-water treatment is that the film of bluestone coating the seed is removed, and the grain is afterwards easily re-infected by stray spores or broken bunt-balls in the drill, unless due precautions have been taken.

Formalin Treatment.*

Formalin is the trade name given to a solution in water of a colourless pungent gas known as formaldehyde, and the solution ordinarily used contains 36 to 40 per cent. of the gas. One pound of formalin (16 ozs. avoirdupois) of the above strength is added to 40 gallons of water, and the seed is immersed in this solution for five minutes, shaking and moving it about sufficiently to insure the wetting of all the grains. The bunt-balls are also skimmed off as before, or the seed may be pickled on the floor by sprinkling the solution over it at the rate of about 1 gallon to each bushel of grain. It is well turned over while being sprinkled so as to get thoroughly wet, and after being in a pile for two hours, it is ready to be planted in the case of wheat, but in the case of oats and barley the damp grain may be allowed to remain over night, in order to allow the formalin to penetrate the husk. Wheat treated with formalin should be sown within 24 hours of treatment in a seed bed moist enough to insure germination in order to obtain the best results.

In a farmers' Press Bulletin issued in 1904 by the North Dakota Agricultural Experiment Station relating to "The effect of evaporation upon solutions of formaldehyde" such questions are asked as—Must the solution which is made up for treating seed grain all be used up the same day? Will it grow weaker from standing? Must a new lot of solution be made up each day? Does the standard formalin lose strength if left uncorked?

The results of special tests showed that solutions of formaldehyde grow stronger by evaporation, the water being given off faster than the gas. A solution, therefore, which has stood open for a number of days is fully as strong as when first made. While this is so, and the water and methyl alcohol or wood spirit of the solution evaporate first, leaving the formaldehyde, which

* By the new industry of wood distillation, Messrs. Cuming, Smith, and Co. are producing formalin at Warburton, and can provide 1-lb. bottles of 40 per cent. strength (same as Schering's) at 1s. 6d. per lb., packages free.

is stronger; behind, yet this also eventually evaporates, especially in warm places. It is therefore advisable to keep the solution corked, if only to keep the strength even.

Whether bluestone or formalin be used, the treated seed should never be put into old bags unless they have first been dipped in the pickle.

Another precaution to be taken is to skim off any smut-balls as well as imperfect seeds. Of course, the wheat used for seed should be free from smut-balls, but farmers are not always as careful as they ought to be in the selection of seed-wheat. It is well known that while sound grain sinks in water the bunt-balls float. One hundred grains of each were taken of Federation wheat, and while the sound wheat weighed 67½ grains, the bunty wheat was only 24½ grains, or a little more than one-third the weight. The bunt-balls may at first be carried down with the sound grains and remain attached by means of air bubbles, but by constant shaking and stirring they come to the top. In practice it is found that all the bunt-balls do not rise to the surface, but the probabilities are that these are cracked, and so their germinating power will be destroyed by the solution.

Effect of Formalin and Bluestone on the Germination of Seed Wheat.

While either of these substances has given satisfactory results in the treatment of bunt or ball smut, as it is often called by farmers, there is considerable difference of opinion as to their effects upon the grain, both as regards germination and the subsequent growth of the plant. Extensive experiments were conducted to answer this question, extending over five successive seasons, and in the last year, when 20 acres were treated, the seed was sown with a drill, bluestone being used at the rate of 1 lb. to 5 gallons of water, and formalin at a strength of 1 lb. in 40 gallons of water. The result of the treatment was very conclusive, and was stated as follows:—"While the untreated plot contained at least 50 per cent. of smut, careful search over the treated plots failed to reveal a single smutty head. Thus both solutions were equally successful in destroying the bunt, but it was noticeable that the plot treated with formalin looked much better and was a little further advanced."

A special test was made with 1,000 grains each of the same variety of wheat sown at the same time and under similar conditions, the formalin and bluestone treatment being compared as before, with the following results:—

Untreated	..	884 grains germinated
Formalin, 1 lb. in 40 gallons of water	..	740 „ „
Bluestone, 1 lb. in 5 gallons of water	..	606 „ „

The bluestone treatment affected the germination much more injuriously than the formalin, and the plants afterwards did not look so healthy.

In all these experiments, however, the grain was sown not more than a day or two after treatment, but it sometimes happens in the ordinary course of farming that sowing is delayed after treatment owing to the state of the weather, or grain is sown in some cases in anticipation of rain, which does not come, and the question arises—how does the treated grain compare with the untreated under such conditions, when germination does occur? Accordingly, tests were made with varying strengths of formalin and varying periods of sowing after treatment. It may be noted here that formalin exercises a hardening effect upon the grain, which soon becomes bone dry, so that the young germ does not so readily force its way through the skin, while in the case of bluestone there is a fine film of the substance left on the seed after treatment, and this will likely have a preservative and protective effect upon the grain.

When seed was treated with varying strengths of formalin and sown after 24 hours, the results of germination were as follows :—

Untreated	84 per cent.
Formalin, 1 lb. in 40 gallons	77 ,,
,, 2 lbs. in 40 gallons	62 ,,
,, 3 lbs. in 40 gallons	41 ,,

The increased strength of formalin above the normal 1 in 40 decreases the amount of germination in a progressive degree.

But when the treated seed was sown after being kept for varying periods of time our experiments showed, on the whole, that wheat treated with 1 lb. in 40 gallons of water loses its power of germination to some extent at least, after being kept a few days ; that this effect is cumulative for a time at least, but it gradually disappears again after, say, four or five weeks.

The late Mr. Farrer also arrived at practically the same conclusion from his experiments in New South Wales, and he summed up as follows :—

> " (1) Formalin does not exercise an injurious effect upon the vitality of seed grain if it be treated just prior to planting, and the conditions at planting time are favorable for its germination.
>
> (2) It is undesirable (and previous experiments at Lambrigg prove unnecessary) to treat seed-wheat with a stronger solution of formalin than that made by mixing 1 lb. of formalin with 40 gallons (400 lbs.) of water."

It was not considered necessary to carry out the same series of exhaustive experiments with bluestone as with formalin, but grain treated at the rate of 1 lb. in 5 gallons of water actually germinated better, instead of deteriorating, after being kept for nine and fifteen days respectively.

Formalin is a well-known antiseptic, disinfectant, and preservative, and is extensively and most satisfactorily used for the treatment of Stinking smut in both the United States and Canada. From its less corrosive action on the seed and the higher percentage of germination which it yields it has certain advantages over bluestone, and if the seed is sown within 24 hours of treatment in a soil sufficiently moist to insure germination the freedom of the resulting crop from bunt is assured.

Hot Water Treatment.

In addition to various chemical substances, heat has also been employed for the destruction of the spores. At first a dry heat was used for the purpose, but what we now know of the resistance of spores to such a heat makes the success of such a method highly improbable. But the hot water treatment of the seed introduced by Jensen in 1888 has proved highly successful. It is a method, however, which is never likely to become popular with our farmers, since without special conveniences it is rather troublesome, and as the methods already given are simpler and equally effective they are generally preferred. The process consists in immersing the seed in hot water at a temperature ranging between 55° to 57° C. (132 to 135° F.), and then plunging it into cold water, and it is the regulation of the temperature which makes the demands on the care and attention of the farmer. Where a steam jet is available it is easy to regulate the temperature. I will just describe the method, as carried out by myself: Three barrels were used—one with cold water, another with the water heated to about 44° C. (111° F.), and a third in which the temperature was maintained at 55–57° C. The grain was placed in a wire mesh basket made for the purpose, and then dipped into the barrel with water at a temperature of

about 44° C. in order to heat it; then it was transferred to the higher temperature, where it was plunged up and down and shaken from side to side for five minutes, so as to bring every grain into contact with the hot water. Any smut-balls floating on the surface were carefully skimmed off. As it is important to keep the water from falling below 55° C., since less heat would not be so likely to prevent the germination of the smut spores, and from rising above 57° C., since it might injure the grain, I attended to the time necessary for dipping and the thermometer, while another kept continually agitating the grain. At the end of five minutes it was immersed in cold water and then spread out on a clean floor to dry. The grain thus treated germinated well and came away quickly, as the heat and moisture combined seemed to stimulate it.

* * * * * *

It has already been pointed out that while these various methods of treatment afford temporary relief, the only permanent means of overcoming the disease is to secure by breeding or otherwise a race which will be "immune" to the attacks of the parasite. In the case of those smuts which infect the host-plant through the flower, this is seemingly the only means at present known of meeting the difficulty.

III.

LIFE-HISTORIES OF VARIOUS GRASS SMUTS.

PLATE XIV.

A.—Healthy and diseased plants (one-tenth natural size).
B.—Healthy Ear or Panicle (reduced $2\frac{1}{2}$ times).
C.—Smutted Ear (reduced $2\frac{1}{2}$ times).
D.—Sound grains ($\times$ 3).
E.—Smutted grains ($\times$ 3).

C. C. Brittlebank, Phot.

D, E, x 3; A, B, C, Reduced.

A—AMBER CANE, SOUND AND SMUTTED. B—SOUND HEAD.

C—SMUTTED HEAD. D—SOUND GRAINS. E—SMUTTED GRAINS.

CHAPTER XX.

Life-Histories of various Grass Smuts.

Only a few of the smuts occurring on various grasses of economic importance will be noticed here, in which the mode of germination of the spores and infection are known, and a more or less detailed account given of their life-history. There are still a number awaiting further investigation, and among our native grasses practically nothing has been done in the way of preventing the spread of the smuts attacking them, which are sometimes very destructive.

1. Grain Smut of Sorghum.

(*Cintractia sorghi-vulgaris* (Tul.) Clint.)

There are two kinds of smut which occur on sorghum, the Grain smut, so called because it confines itself chiefly to the individual grains, and the Head smut, because it converts the whole head, just as it emerges from the upper leaf into one large smutty mass. The Head smut of maize has already been described, and the same fungus which causes it is also found on sorghum, but not hitherto in Australia. It is the Grain smut which has been found here on broom corn, amber cane, and sugar sorghum, and wherever it occurred was very destructive. The cultivated sorghums are placed under *Andropogon sorghum*, Brot., by Hackel, of which there are a number of varieties, such as broom corn, amber cane, and sugar sorghum, the latter variety being usually called *Sorghum saccharatum*, Pers.

Effects and Losses.

The effects of this smut upon the host-plant is very noticeable in preventing the formation of seed. The seed is replaced by an enlarged body of a dirty white or brownish colour, splitting irregularly at the top and exposing a mass of dark-brown spores. In a crop of sugar sorghum examined in March there were about 14 per cent. of the plants affected (1 in every 7), while amber cane grown in the same field was only slightly affected.

The smutted ears or panicles are readily recognised in the field, from the grains being replaced by a horn-like projection of a dirty white or brownish colour. The individual smut bodies are not only considerably elongated, but usually somewhat stouter than the normal healthy grains (Plate XIV.). The ear may be attacked by the smut even while still green, and a portion of it only in flower. Occasionally there may be a few clean grains on an otherwise smutty ear. In the case of broom corn the loss is not so serious as where the sorghum is raised for seed. Nevertheless, the brush of an infected plant is of an inferior grade, and almost worthless. In healthy broom corn the rays are uniform in thickness and length, and all spring from nearly the same point, but in infected plants the rays are of unequal length, and arise from an elongated and thickened central axis. The number of large rays, too, are always less, so that the commercial value of the brush is lessened. One prominent grower stated that most of the heads that have smut on them are of no account.

The monetary loss from this smut is considerable, since the crop is so valuable. Amber cane, when it is grown for seed, may sometimes be worth £25 to £30 per acre, so that the loss is serious enough to render preventive treatment desirable.

Distribution.

It occurs in Southern Europe, Asia, Africa, and America, as well as in Australia. It was brought to the United States through imported seed, and, no doubt, it was also introduced here in the same way. I have examined seed of amber cane and sugar sorghum obtained from the best seedsmen, and in every instance the spores of the smut were present, even although it appeared to be quite clean, as from the mode of hand-picking the seed and winnowing, none of the smut bodies were found. Is there any wonder, then, that the smut, from being a negligible quantity, should be gradually on the increase, when the spores are regularly sown with the seed, without any treatment ?

Germination.

The spores germinate readily in water. Fresh spores were taken in February, and in twelve hours there was vigorous germination. They retain their germinating power for a number of years, and De Bary states that Liebenberg germinated them after being in the herbarium for six and a-half years.

The germination has been described by Brefeld, Clinton, Norton, and others. The spore puts forth a promycelium, which divides into three or four cells by transverse septa. Quite a feature of the promycelium is the formation of the so-called buckle or knee-joints. A short out-growth arises at the end of one or more cells, and this bends over and unites with the adjoining end of the next cell. From these protuberances or from the end of the promycelium slender filaments of varying length grow out, called by Clinton infection threads, on account of their supposed function. Conidia are generally produced either from the tip of the promycelium or at the apex of the cells and readily fall away from their connexion.

In a nutrient solution the germination was more luxuriant and the formation of conidia was increased.

Infection.

This takes place in the seedling stage, and may either occur by means of infection threads from the promycelium itself or from conidia. These threads must reach the growing tip of the plant in order to infect successfully, and that is only possible when the cells are young and tender. Whenever the young plant appears above ground it is then proof against infection.

Spore Formation.

A cross-section of a young infected ovary shows a central core of plant tissue or columella, a firm outer wall, and the spores between. The outer membrane is composed of a more or less distinct epidermis with a layer of fungus cells beneath, which may attain a thickness of 40 μ. The spores are fully formed on the outside nearest the fungus layer and gradually become immature towards the centre. If the spores are traced from the columella they begin to be formed just outside the fibro-vascular bundles. The fungus filaments seem to have gelatinized their walls, and the protoplasmic contents

appear as colourless, amorphous bodies. These radiating strands become more distinct towards the outside, and their cell-wall is firm and tinted. The spores begin to take shape, and are at first colourless, but gradually assume the olivaceous colour and the globose shape of the mature spores, which are densely packed. In this way all the spores gradually become mature and the diseased grains remain mostly unbroken unless knocked about in harvesting.

¶ The spores are thus seen to be formed, not simultaneously in the fertile hyphae, but in a progressive manner towards the centre, and this mode of formation of spores is characteristic of Cintractia.

Treatment.

Clinton[1] found hot water treatment of the seed to be a preventive. Field experiments also showed "that the amount of smut ordinarily occurring in broom corn can be greatly increased by mixing a liberal supply of the smut with the seed before planting, but was not increased by planting seed in land that had smut in it or by placing smut on the plants after they appeared above ground."

No matter whether ordinary or badly smutted seed was treated, the smut was practically prevented. Freeman and Umberger[1] have also proved by experiment that formalin, hot water, or bluestone give satisfactory results.

2. Brome Grass Smut.

(*Ustilago bromivora* (Tul.) F. v. W.)

Brome smut has been found here on soft brome (*Bromus mollis*, L.) and prairie grass (*Bromus unioloides*, Humb.), both of which are imported, and on sand brome (*Bromus arenarius*, Labill.), which is a native of Australia and New Zealand. It is very general and widespread in its distribution. The

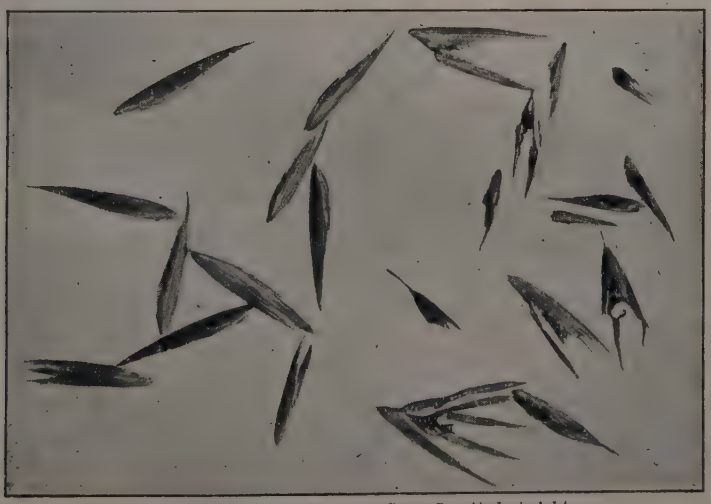


Fig. 14.—Prairie Grass Seed.—Some Smutted at right.

soft brome is sometimes so badly attacked that there is hardly a sound ear in hundreds of acres. The sheep feeding in such paddocks are sometimes black

over a large portion of their bodies from the spores, clouds of which rise in the air as the flock walks through the grass, and yet, according to Brefeld, it is rarely found on this species in Europe. It is also sometimes very bad on the prairie grass, not only destroying the grains but even the base of the glumes (Plate XV.). In the early part of 1907 the attack was particularly severe, and in some paddocks of this grass every plant was infected.

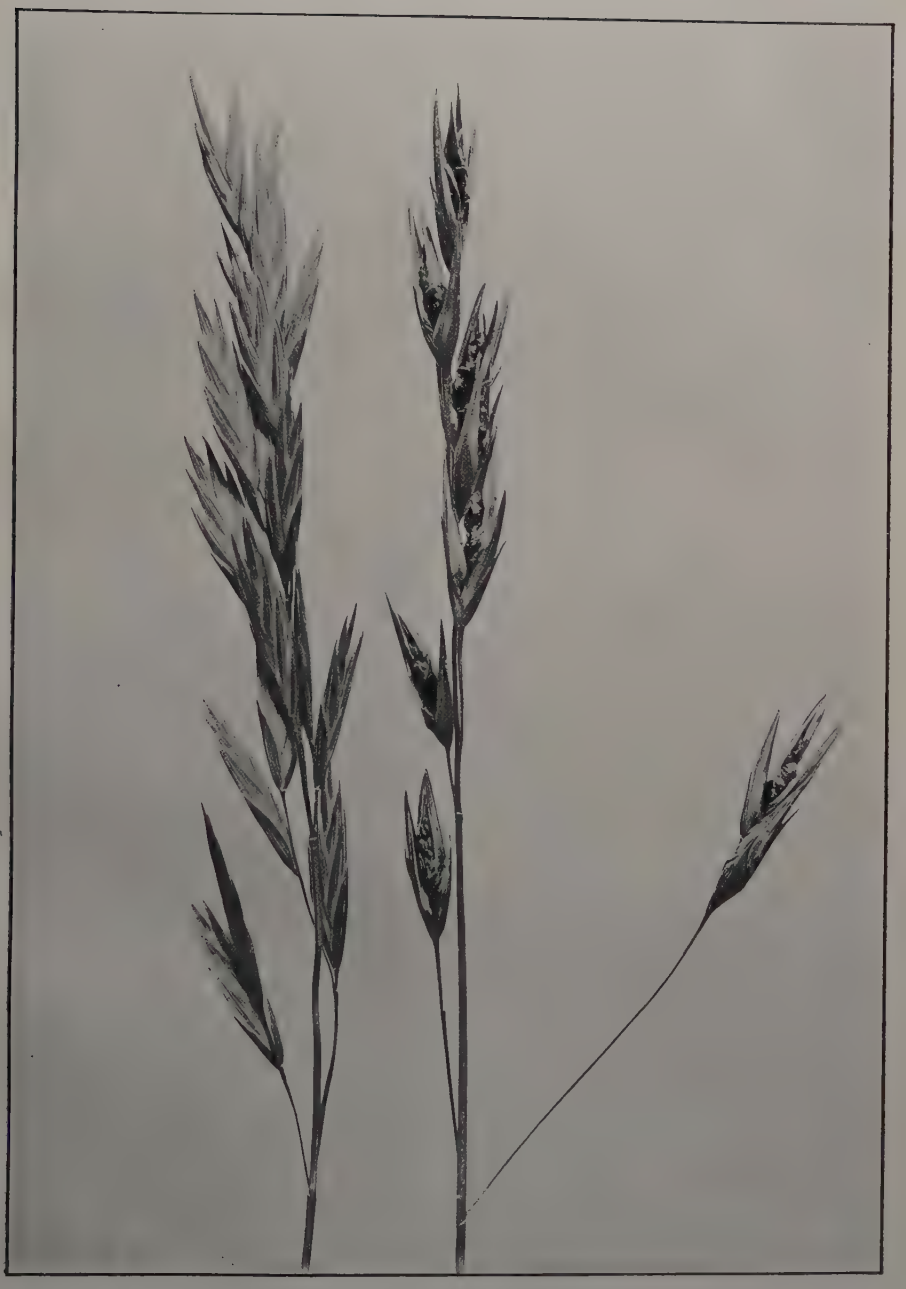
In 1908 it became something of the nature of an epidemic, and this splendid winter fodder grass, the seed of which is now on sale in Britain for this purpose, was very badly affected in various districts of Victoria, where it forms the principal pasturage. How it is spread may be seen from the accompanying figure, which shows a sample of seed brought under my notice when the farmer found all his crop smutted. On visiting this paddock I found that not a single plant had escaped, and recommended burning to destroy the spores. But the farmer preferred to utilize it as fodder, and so turned his cows into it, and they also fed upon the cut hay without any seemingly injurious effects. Such diseased plants have sometimes been reported to be poisonous, but they were evidently not so in this instance. This was in 1907; and last year he informed me that any heads which sprung from the self-sown grass were just as smutty as before. It will be rather a difficult task to get rid of it now, seeing that the spores retain their vitality for years, but root and other crops are being grown instead of grass. The seed referred to was sold to the farmer by leading seedsman, and such a case emphasizes the necessity for some means of preventing such seed being sold without inspection.

Fig. 15.—Upper portion of panicle showing diseased spikelets at base and healthy at top.

At first the glumes are leaden-coloured and enclose the spores, but the glumes gradually become disrupted and allow the spores to escape. Occasionally in the prairie grass several stalks are found springing from the same root, of which one may be quite free from smut, while the others are diseased.

Germination.

The spore germinates freely in water, and retains its germinating power for some time. I gathered soft brome with this smut in November, 1904, and in July, 1906, it was still capable of germination. Then in May, 1907, spores from the same plant germinated in water, so that they still retained their germinating power for at least two and a-half years. The spores put forth a small germ-tube or promycelium, and this bears at its apex a conidium, which is soon detached. The conidia are colourless, elongated, cylindrical, flat at attached end, rounded at free end, $13-17 \times 3-4\ \mu$.



G. H. Robinson, Phot. Nat. Size.

BROME GRASS SMUT ON PRAIRIE GRASS

(*Ustilago Bromivora.*)

In a nutritve solution Brefeld found that the spore puts forth a germinal tube, which is larger and more robust than that produced in water. It soon divides into two cells, and this short promycelium produces conidia. These conidia soon fall away, increase in size, and become uniseptate and behave like the promycelium from which they sprung in producing secondary conidia, hence Brefeld calls them bicellular sporophores. This formation of primary promycelia from the spore and of secondary promycelia from the conidia continues until the nutritive solution becomes exhausted. In more dilute nutritive solutions the promycelium itself as well as the sporophores give off mycelium-like tubes, and fuse in various ways.

U. bromivora is thus characterized by its conidia growing into bicellular sporophores, which sprout directly into new conidia. True sprouting conidia do not occur.

Infection.

When seed is sown with adherent spores infection readily occurs, and in a favorable season the smutted seed produced plants in which not a single one escaped the disease. In this instance the seed was not artificially infected, but just as it was received from the seedsman (Fig. 14), and it shows how efficient this mode of infection must be in this particular species of smut.

Treatment.

When the seed is treated with bluestone or formalin, as in the case of bunt, the spores are destroyed and no infection occurs.

3. Kangaroo Grass Smuts.

(*a*) *Cintractia exserta*, McAlp.;
(*b*) *Sorosporium enteromorphum*, McAlp.;
(*c*) *Tolyposporium bursum* (Berk.) McAlp.

There are three smuts known on the Kangaroo grass in Australia belonging to the three genera of Cintractia, Sorosporium, and Tolyposporium respectively. They are not as yet known to do much damage, except in certain districts, but that may be simply owing to the fact that they have hitherto escaped notice. They are all confined to the spikelets, distorting and destroying them.

(*a*) The Cintractia smut is very characteristic, since it stands out from the glumes as an elongated greyish membrane enveloping the spores and the long rigid awn of the healthy plant has generally disappeared (Plate XVI., B, C.). When a cross-section is made towards the base of a diseased spikelet the formation of the spores is clearly seen. There is a central core of plant tissue, and surrounding this is a colourless mass of fungus filaments, from which the spore-forming hyphae proceed. As the spores are formed inside, from the centre outwards, the walls of the hyphae deliquesce and become gelatinous, and the final result is that a dense mass of spores is formed inside the enveloping membrane. This membrane gradually decays and the mature spores are exposed.

The germination of the spores has not been observed.

(*b*) The Sorosporium smut has received its specific name from the elongated and puckered membrane which encloses the spores, being often twisted upon itself, and resembling the intestine (Plate XVI., A.). The spore-balls are composed of spores which hang loosely together, and they ultimately escape by the decay of the membrane.

Their germination is not known.

(*c*) The Tolyposporium smut is readily recognised from the sac-like yellowish membrane enveloping the spores (Plate XVII.). The spore-balls are very black, and the spores are firmly and permanently united. They germinate readily in water, even after being kept for four years, and produce a promycelium which bears lateral and terminal conidia. When the conidia are detached they bud in a yeast-like manner.

4. Wallaby Grass Smuts.

(*a*) Black Smut (*Ustilago readeri*, Syd.)

(*b*) Bronze Smut (*Ustilago comburens*, Ludw.)

(*a*) The black smut is fairly common on various species of Danthonia or Wallaby grass, and is found on the leaves as well as in the inflorescence. It has been known for a considerable time, although only recently named by Sydow, who recognised it as a new species. It had been previously named by Cooke *U. destruens*, Schlecht.

It is a very conspicuous smut, as the entire inflorescence is invaded by it. The glumes may remain, enclosing the blackened mass, but even they are sometimes partially or entirely destroyed (Plate XVIII.). In its early stages the diseased inflorescence is enveloped by the leaf-sheaths, but these soon fall away and expose the black powdery mass of spores. On the leaves and sheaths it also forms conspicuous lines, and altogether it is so destructive that the grass is completely wiped out in patches.

Germination.

The spores germinate very readily in water, either immediately on maturity or some time after. At the end of two years, however, only an occasional spore is capable of germination. They produce an elongated promycelium bearing lateral and terminal conidia, but their subsequent history was not followed. No doubt, these conidia produce a delicate germ-tube, which penetrates the young seedling and thus causes infection.

(*b*) The bronze smut is easily distinguished by its bronze-green colour, in contrast to the other, which is black (Plate XIX.). It occurs in the upper portion of the stem, as well as in the inflorescence, which it ultimately completely destroys. The spores are exceedingly numerous and very minute. and, although at first agglutinated together, they soon become powdery.

Germination.

This was not very successful. Fresh spores were placed in a Petri-dish with water, and after nine days a few of them produced a one-septate promycelium, but there was no further development.

G. H. Robinson, Phot. Nat. Size.

TWO KANGAROO GRASS SMUTS

(*A—Sorosporium Enteromorphum.* *B, C—Cintractia Exserta.*)

G. H. Robinson, Phot.

Nat. Size.

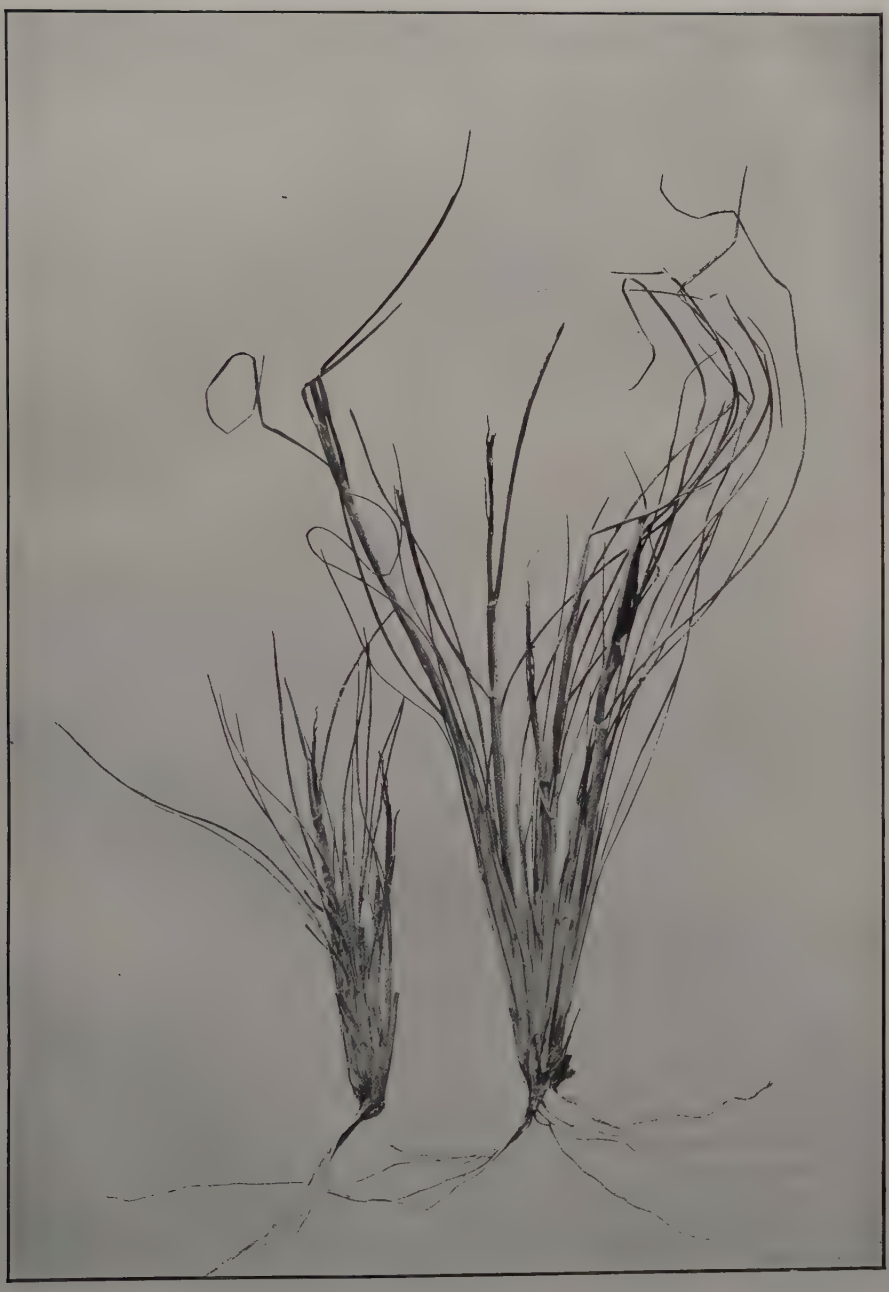
A KANGAROO GRASS SMUT

(*Tolyposporium Bursum*).

G. H. Robinson, Phot. Nat. Size.

BLACK SMUT OF WALLABY GRASS

(*Ustilago Readeri.*)



G. H. Robinson, Phot. Nat. Size.

BRONZE SMUT OF WALLABY GRASS

(*Ustilago Comburens.*)

IV.
FIELD EXPERIMENTS.

CHAPTER XXI.

Field Experiments during Season 1909.

The most appropriate place to give an account of the experiments just completed for 1909, seemed to be at the close of a general study of the Smuts, and before entering upon the consideration of their classification. There were various questions of a practical nature which arose in connection with the treatment and behaviour of the cereal smuts, and these required an answer, even although that answer in many cases could only be fully and finally given after further and continued experiment. A general idea of some of these may be briefly given.

There were several preparations on the market for the treatment of smut and other diseases, and it became necessary to test them in comparison with such recognised substances as bluestone and formalin.

Then it was desirable to know how far the different species and sub-species of Triticum were liable to bunt, so that in crossing there might be some guide as to those which were most immune under our conditions.

Again, a number of the crosses made by Mr. Pye at Dookie Agricultural College, with Medeah blood in them, seemed to resist the bunt there better than many others, and various selections were chosen for trial to see how far this resistance to bunt was a hereditary quality. Of course, these experiments will require to be continued in order to settle the point satisfactorily.

There were also some doubts as to the relative virulence of the disease of Flag Smut of wheat when the seed was sown in clean ground with the spores of the fungus upon it, and when clean seed was sown in ground containing the diseased straw from a previous crop.

And finally, there were a number of previous experiments which required to be repeated in order to see the effect on the result of different weather conditions. From the extent and variety of these experiments it was only convenient to use small plots, and while the actual results obtained will require corroboration on a larger scale, still the relative results are of considerable value, as indicating at least in what direction the truth lies. The information obtained can generally be put in the form of Tables which will show at a glance the essential points determined.

A Comparison of Various Fungicides for Bunt.

A sample of the powder known as "Fungusine" was supplied to us for trial, and the chemist for Agriculture reported after analysis that the substance consisted principally of ordinary burnt lime, white arsenic, and crude phenyl. This preparation was used, as well as phenol, and a comparison was made between these two substances and bluestone and formalin respectively as smut preventives. A variety of wheat from Tasmania was chosen for treatment, naturally infected as it came from the machine, and it was certainly as smutty a sample as had ever come under my notice. The seed wheat was all treated at the same time and sown on the same day (28th June) in ground which was as nearly as possible equal throughout. The formalin and bluestone were used as already recommended, while the fungusine was applied to the seed according to the instructions given, and the phenol was a 2 per cent. solution. 500 grains were sown in each plot, arranged in rows of 100 each, and the results were taken on 30th December, when the wheat was fully ripe.

TABLE VII.—FUNGUSINE AND PHENOL COMPARED WITH BLUESTONE AND FORMALIN AS FUNGICIDES.

Plot.	Grains Sown.	Grains Germinated.	Treatment.	Percentage of Germination.	Percentage of Bunt.
1	500	405	Fungusine ..	81	78 plants = 19.2
2	500	363	Bluestone ..	73	8 ,, = 2.2
3	500	339	Formalin ..	68	28 ,, = 8.2
4	500	355	Phenol ..	71	68 ,, = 16.3
5	500	428	.. ..	85	379 ,, = 88

We are now in a position to compare the relative effects of fungusine, bluestone, formalin, and phenol, when used as a dressing for bunt-infected seed, and it will be convenient for purposes of comparison to fix the numerical relation between the effect of treatment with a particular substance and that of untreated seed. Thus, in the case of fungusine, there was 88 per cent. of bunt in the untreated plot, and 19.2 per cent. in the treated plot, so that if the one is divided by the other it gives the numerical relation between the two and fixes a standard of comparison $\frac{88}{19.2} = 4.5$. This number represents the factor or *co-efficient of efficiency* for fungusine.

If the other treatments are dealt with in the same way then the following is the result :—

CO-EFFICIENTS OF EFFICIENCY.

Bluestone	40
Formalin..	10.7
Phenol	5.4
Fungusine	4.5

Thus, bluestone is nine times more effective than fungusine in the prevention of bunt, and even phenol, when used alone, without the other ingredients entering into the composition of fungusine, is slightly more efficacious. Apart altogether from the relative efficiency of the various substances used, the fact stands out prominently of the great saving effected in comparison with no treatment at all, although, of course, no intelligent farmer would ever dream of sowing such a smutty sample of seed.

THE DIFFERENT SPECIES AND SUB-SPECIES OF "TRITICUM" IN RELATION TO BUNT.

In the quest for a smut-resistant wheat to be used as one of the parents in crossing, the necessity for testing different kinds is evident. Accordingly, I obtained from Germany samples of all the known cultivated species and sub-species, which are classified by Hackel, as follows :—

Triticum
- *monococcum* L., Einkorn or One-grained Wheat.
- *sativum* Lam.
  - *dicoccum* Schrank, Emmer.
  - *spelta* L., Spelt.
  - *tenax*
    - *vulgare* Vill., Common Wheat
    - *compactum* Host, Club or Dwarf Wheat.
    - *turigdum* L., Poulard or Rivet Wheat.
    - *durum* Desf., Durum or Hard Wheat.
- *polonicum* L., Polish Wheat.

The seed was of varying ages, so that in some cases so few grains germinated that the results were useless for comparison; but my friend Professor Patrick Wright, of the West of Scotland Agricultural College, has sent me fresh specimens which will be carefully tested in the forthcoming season.

TABLE VIII.—RELATIVE SUSCEPTIBILITY TO BUNT OF THE DIFFERENT SPECIES AND SUB-SPECIES OF TRITICUM.

Plot.	Species or Sub-species.	Grains Sown.	Grains Germinated.	Treatment.	Percentage of Germination.	Percentage of Bunt.
6	Triticum vulgare .. (Ordinary Wheat)	25	14	..	56	—
7	,, ,, ..	25	16	*Tilletia levis*	64	11 plants=68.75
8	Triticum turgidum	25	17	..	68	—
9	,, ,,	25	0	*Tilletia levis*	..	—
10	Triticum spelta ..	25	5	..	20	—
11	,, ,, ..	11	4	*Tilletia levis*	36.3	—
12	Triticum polonicum	20	7	..	35	—
13	,, ,,	20	5	*Tilletia levis*	25	—
14	Triticum monococcum	18	14	..	77.7	—
15	,, ,,	18	8	*Tilletia levis*	44.4	—
16	Triticum durum ..	25	2	..	8	—
17	,, ,, ..	25	1	*Tilletia levis*	4	—
18	Triticum dicoccum	25	9	..	36	—
19	,, ,,	10	5	*Tilletia levis*	50	3 plants = 60
60	Triticum compactum	25	24	..	96	—
61	,, ,,	25	25	*Tilletia levis*	100	24 plants = 96

NOTE.—The seed of T. compactum was quite fresh, as it was grown at Burnley Horticultural Gardens the previous season.

No definite conclusions can be drawn as to relative susceptibility, since the proportion of plants which grew were sometimes so few as to constitute a negligible quantity. In the case of *T. compactum*, there is no doubt of its being very liable, and the solitary plant which escaped infection grew to a height of 4 ft. 6 in., which was the average of the clean plot, while the general average of the bunted plants was 3 ft. 6 in. The smut had evidently affected the growth injuriously to the extent of 1 foot, and the seed from the one plant which escaped infection will be sown again.

SELECTIONS FROM CROSSES TESTED FOR SUSCEPTIBILITY.

In the results of experiments at Dookie Agricultural College by Mr. Pye, recorded at p. 52, it is shown that selections from his numerous crosses were, in many cases, free from bunt after infection, especially those in which Medeah, one of the Durums, was used as one of the parents. Mr. Pye kindly supplied me with a number of the more promising selections for trial under the conditions prevailing at Burnley Horticultural Gardens to test how far the smut-resistance was hereditary and retained this quality under different conditions of soil and climate, heat and moisture. The rainfall at the two Experiment Stations throughout the year is given here for comparison.

RAINFALL AT DOOKIE AGRICULTURAL COLLEGE FOR 1908 AND 1909. POINTS.

Year.	Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Total.
1908	24	54	58	23	199	436	137	169	260	150	75	47	1,632
1909	44	72	152	257	321	369	191	363	183	86	17	37	2,092

RAINFALL AT BURNLEY HORTICULTURAL GARDENS FOR 1909, AND AVERAGE. POINTS.

Year.	Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Total.
1909	324	147	119	192	314	327	120	359	185	161	61	277	2.586
Average	188	172	213	238	211	209	185	180	231	268	224	224	2,543

The sowing took place at Dookie in June, 1908, and at Burnley in June, 1909. For the first four months, at Burnley, the rains were about the average amount. The next four months—May to August—constituted a very wet period, which culminated in the greatest general flood ever experienced in Victoria. The abundant rains at the sowing season insured the germination of the seed and the spores, and consequent infection by the fungus where the seed was not treated.

TABLE IX.—SELECTIONS FROM CROSSES TESTED FOR SUSCEPTIBILITY TO BUNT.

Plot.	Cross.	Selection.	Grains Sown.	Grains Germinated.	Infection.	Percentage of Germination.	Percentage of Bunt.
31	Tripola ..	7	25	17	..	68	—
	Bobs × Medeah						
32	,, ..	7	25	16	*Tilletia levis*	64	7 plants = 43.7
33	,, ..	8	25	17	..	68	—
34	,, ..	8	25	17	*Tilletia levis*	68	13 plants = 76.4
35	,, ..	9	25	23	..	92	—
36	,, ..	9	25	23	*Tilletia levis*	92	21 plants = 91.3
37	Bobs × Medeah	10	25	20	..	80	—
38	,, ..	10	25	23	*Tilletia levis*	92	21 plants = 91.3
39	,, ..	11	25	22	..	88	2 plants = 9
40	,, ..	11	25	24	*Tilletia levis*	96	23 plants = 96
41	,, ..	12	25	24	..	96	—
42	,, ..	12	25	19	*Tilletia levis*	76	17 plants = 89.4
43	,, ..	13	25	23	..	92	—
44	,, ..	13	25	21	*Tilletia levis*	84	20 plants = 95.2
45	,, ..	14	25	22	..	88	—
46	,, ..	14	25	24	*Tilletia levis*	96	24 plants = 100
63	Medeah ..	..	25	15	*Tilletia levis*	60	7 plants = 46.6

The percentage of bunt varied from 43 to 100 where the seed was infected, and only in one instance did the uninfected seed show any trace of the disease. Medeah, which was bunt-proof at Dookie in 1908, turned out to be quite susceptible with us in 1909, having 46.6 per cent.

Results of Infection without Treatment.

It has already been shown in Table VII. that wheat may be naturally infected with the spores of bunt so as to yield 88 per cent. of infected plants, but when artificially infected it may even reach 100 per cent. This severe infection is employed both in testing the capacity of different varieties for withstanding the bunt as well as the effect of different kinds of treatment, both before and after infection. In the following table it is shown that both *T. levis* and *T. tritici* may produce complete infection, and that when a smut-ball is sown along with each uninfected grain there may be as much as 88 per cent. of diseased plants produced :—

Table X.—Results of Infection without Treatment.

Plot.	Variety.	Grains Sown.	Grains Germinated.	Infection.	Percentage of Germination.	Percentage of Bunt.
22	Federation ..	25	23	.. .. ..	92	2 plants = 8.7
23	„ ..	25	25	Smut-ball in contact with each grain	100	22 „ = 88
30	„ ..	25	20	*Tilletia levis* ..	80	19 „ = 95
58	„ ..	25	20	.. .. ..	80	—
72	„ ..	25	25	.. .. ..	100	2 „ = 8
74	„ ..	25	14	*Tilletia levis* ..	56	14 „ = 100
70	„ ..	25	25	„ ..	100	25 „ = 100
71	„ ..	25	20	*Tilletia tritici* ..	80	20 „ = 100
56	Ohio ..	25	24	.. .. ..	96	—
57	„ ..	25	23	*Tilletia levis* ..	92	1 plant = 4.3
20	Genoa ..	25	24	.. .. ..	96	—
21	„ ..	25	22	*Tilletia levis* ..	88	1 plant = 4.5

In two of the plots of Federation wheat, where the grain was sown without artificial infection, there was 8 per cent. of infected plants, so that the wheat to begin with was not perfectly clean.

Plots 70 and 71 were specially sown, and the grain infected with *T. levis* and *T. tritici* respectively, in order to compare the resulting growth. It is stated at p. 55 that Harwood found *T. levis* to have the effect of shortening the straw and stunting the growth, while no such effect was produced by *T. tritici*, but in this instance the very reverse was the case. The plants infected with *T. levis* averaged 3 feet in height, but with *T. tritici* they were only $2\frac{1}{2}$ feet. No striking difference was generally noticeable, however, between the infected and uninfected plots, as it is usually when the grain is forming and not while the plant is growing that the effect of the parasite begins to be outwardly visible.

It will be observed that the Ohio and Genoa varieties were subjected to the same severe trial as Federation, and that only a little over 4 per cent. of the plants were affected in each case. It will be remembered that Ohio wheat is one of those varieties which germinates rapidly, and is, therefore, supposed to be less susceptible to bunt on that account, and the result of further experiment bears this out. The strain of Genoa was chosen for further trial, because it was absolutely free from Stinking Smut the previous season, and the seed from clean plants of both Ohio and Genoa will be sown the coming season. In both varieties only one plant was bunted and only a single ear in each.

There are at least two methods for securing bunt-resisting plants, and both lines of investigation are being followed. The one is to cross resistant with non-resistant varieties, and thus secure in the hybrid the desired quality. The other is to select the seed of resistant individuals for propagation, and while the latter is the easier of the two, it is only likely to hold for the locality in which the selection is made; but in the other the quality, when secured, is likely to be more permanent and independent of its immediate environment.

Entirely and Partially Bunted Plants.

As bearing on the amount of loss caused by this smut, it is interesting to inquire whether the ears in affected plants are generally all destroyed or only a portion of them. It has been already shown at p. 78, that smutty and sound ears in the same plant is the general rule, and I had abundant opportunity of verifying this fact during the past season. Taking a plot of Federation wheat as an example, in which every plant grown was bunted, it was found that when infected with *Tilletia levis* there were seventeen plants entirely and eight only partially bunted, while with *T. tritici* there were fourteen plants entirely and six partially bunted, or nearly one-third with the stool only partially infected. In some cases therefore there may be even a greater proportion of plants entirely bunted than only partially so.

Field experiments with Flag Smut (*Urocystis tritici*) have already been recorded at p. 98, showing the effects of seed treatment. It is not uncommon to find with this smut that the entire stool has not produced a single ear, as is only too evident to the farmer in his general crop, and the consequent disappointing yield in a season when this disease is prevalent. Thus, in a plot of Federation wheat, where infected grain was sown, nearly 17 per cent. of the affected stools were without ears.

Relative Effects of Bluestone and Formalin on Germination, Infection, and Yield.

As an object-lesson for farmers, five plots were sown under ordinary farming conditions at Longerenong Agricultural College with wheat of the variety Jade, which had a little smut with smut-balls scattered through it.

Each plot was carefully laid out and measured, and contained .776 of an acre.

The seed was sown at the rate of 50 lbs. per acre, and one lot was treated with bluestone and formalin respectively on 12th March, 1909. Formalin (40 per cent.) was used at the rate of 1 lb. avoirdupois to 40 gallons of water or 1 in 400, and bluestone at the rate of 1 lb. to 5 gallons of water, or a 2 per cent. solution. This was done to test the effect of treating the grain some considerable time before sowing. Another lot was treated similarly on 17th June, and the whole was sown on the 28th of the same month. The earlier treated wheat was left in the bags side by side on the barn floor, with a couple of sticks beneath to prevent their touching the brick floor, and they were still moist at sowing time, but dried before being placed in the

seed-drill. Both bags were thus kept under exactly similar conditions after treatment, but the bluestone-treated seed was mouldy, and a large proportion of the grains soft and rotten, while that treated with formalin was a little mouldy, but there were much fewer rotten grains than in the other.

The plots were critically examined on 9th December, and afterwards stripped with the following result :—

TABLE XI.—TREATED AND UNTREATED BUNTY WHEAT, COMPARED AS TO GERMINATION, INFECTION, AND YIELD.

Plot.	Seed Treatment	Date of Treatment.	Gross Yield.		Yield per Acre.		Percentage of Bunt.
			bus.	lbs.	bus.	lbs.	
1	Bluestone ..	12th March, 1909	1	39	2	7	—
2	Formalin ..	,, ,,	6	59	9	0	(1 plant affected)
3	Untreated ..	.. .. ..	15	12	19	35	.85
4	Bluestone ..	17th June, 1909	11	55	15	21	(1 plant only affected)
5	Formalin ..	,, ,,	12	47	16	28	—

The experiments are at least suggestive, if not conclusive, and, as far as they go, they are strictly comparative.

In Plot 1 the seed was so rotten that no one would think of sowing it but for experimental purposes. The crop was very inferior, and the plants so scattered that they were only stripped for comparison.

In Plots 4 and 5 the treated seed was kept for eleven days before sowing on account of the weather, and the results of germination were relatively similar to that already recorded on p. 115.

The treatment was practically effective in preventing the bunt, only one diseased plant being found in the earlier formalin-treated and later bluestone-treated plot respectively. In the untreated plot, the bunt was only .85 per cent., the amount being calculated by counting the diseased plants in several rows, then estimating the number of plants in a row, and this multiplied by the total number of rows in the plot, gave the number of plants altogether, and from the number of diseased plants in each row the percentage was determined.

There is one outstanding fact in all the experiments for treating the grain on a large scale—that the untreated gives a superior yield to the treated, the same amount of seed being used in each case. This shows the necessity for so improving the treatment, that, while destroying the spores of the smut, it will not impair the vitality of the seed. Experiments by Messrs. Sutton and Pridham[1] have shown the ameliorating effect of lime after bluestone, but a fungicide which is fatal to the spore while stimulating to the seed is still a desideratum.

The loss caused by disease in crops must be very large in the aggregate, and, as Mr. Pye[1] has remarked in his article on Diseases and Pests in Cereals —"If statistics could be published of the financial loss to the State, due to the ravages of fungoid and allied pests, the amount would be astounding." It is practically impossible to obtain exact data of the loss caused by diseases

of this nature, and estimates are only approximate, but, by giving the estimates made by responsible authorities for bunt of wheat and smut of oats alone, in certain countries, it may be brought home to the farmer what a saving would be effected by simply treating his seed in the way experience has proved to be efficacious.

Crop.	Disease.	State.	Period.	Estimated Loss.	Authority.
				£	
Wheat	Stinking smut (*Tilletia levis* and T. *tritici*)	Victoria ..	1898	50,000	McAlpine
..	,, ,,	Ohio ..	Annual	52,083	Selby
Oats ..	Smut (*Ustilago avenæ*)	Kansas ..	1888	287,985	Kellerman and Swingle
.. ..	.. ..	.. ..	1889	177,199	Kellerman and Swingle
.. ..	.. ..	.. ..	1890	189,854	Kellerman and Swingle
.. ..	.. ..	Indiana ..	1889	166,151	Arthur
,, ..	.. ..	.. ..	1890	126,115	Arthur
.. ..	.. ..	Michigan	1891	166,666	Harwood
.. ..	,, ..	..	1892	208,333	Harwood
,, ..	.. ..	Wisconsin	1901–3	2,812,500	Moore
.. ..	.. ..	United States	1880–1890	33,845,210	Swingle
,, ..	.. ..	..	Annual	3,384,521	Swingle

V.

CLASSIFICATION AND TECHNICAL DESCRIPTIONS.

CHAPTER XXII.

Classification.

It is often hinted, or evenly plainly stated, that the systematic classification of Fungi is neither necessary nor useful where the object in view is to investigate diseased conditions due to parasitic fungi. It is contended that the physiology and not the morphology is the important thing, that if the life-history is clearly traced and the abnormal conditions properly studied, nothing further is required for a correct diagnosis of the disease. This may be true for isolated instances, but where the diseases of plants are comprehensively studied, and, particularly in a continent like Australia, where the fungus-flora is not as yet too well known, I consider it to be indispensable for a proper appreciation of the nature and effects of the diseased conditions, that the nature and affinities of the organisms causing them be definitely known and defined if possible. As the President of the Field Naturalists' Club of Victoria remarked in his annual address for 1907—"In a new country, until your objects have been collected in fairly large numbers, and dealt with from a systematic point of view, it is difficult to see on what lines to investigate the steps in their individual life-histories." In fact, until their affinities are known, comparative study is impossible.

In the first place, if the parasite should happen to be a new one, it will be a guide in our investigations to know how it is related to other forms, as well as its modes of reproduction and so forth. In the next place, if it is not a new one, its exact determination will enable us to learn what is known about its habits and history, and possibly serve as a guide to some method of treatment. In the third place, when it has been determined and catalogued, it will enable the future investigator readily to know when he is dealing with the same disease, and afford him valuable hints in tracing its course. In the literature of Plant Pathology one often meets with more or less elaborate descriptions of diseases, such as a Wheat disease, a Potato disease, or a Lily disease, without a clue to the definite parasite, and in such diseases there is often a doubt as to the distribution of the disease, and where the symptoms vary somewhat there is difficulty in deciding as to its identity. When the smut of maize was first discovered in Australia, it was naturally concluded to be the corn smut common in America, and named accordingly, but when its systematic position was settled it was found to be quite a different smut, and while in some cases the determination of the fungus may not help us much in the way of treatment, in others, where its nature and mode of attack are known, it may afford a clue of considerable value.

In short, there are at least four factors to be considered in the study of any particular parasitic disease—(1) the organism which is parasitic upon the plant, (2) the plant which is attacked, (3) the predisposing causes which have favoured the entrance of the parasite into the plant, and (4) the mutual reactions of plant and parasite.

The members of this group of parasitic fungi are, as a rule, easily recognised by the production of soot-like masses of spores, and while these may be formed in any portion of the host-plant, the special parts in which they occur are usually constant for each species, and this is frequently the ovary which is thereby completely converted into a mass of spores. The reason for the ovary being so often chosen for this purpose is probably owing to its being such a splendid situation for the dissemination of the spores.

It may also be chosen because it is a perfect store-house of nourishment provided by the young embryo in a form easily assimilated, so that the parasitic fungus steps in and utilizes for its own reproduction what was originally intended for the propagation of the species of the host-plant.

The most prominent feature of the smuts is their reproductive bodies or spores, and they form the basis of our classification, taken in conjunction with their mode of formation and germination. In fact, so important a systematic character is the mode of germination of the spore that it is used to divide the group into two main divisions, and in cases where this has not been observed, there is often room for doubt as to the exact position of the species. The spore, on germination, puts forth a germinal tube, which may either divide transversely and form lateral as well as terminal conidia, or it may remain at first undivided and produce a crown of conidia at the apex. Too much stress must not be laid on the undivided germinal tube, for it is the whorl of conidia at the apex which is the distinctive feature. This is the basis of the main division of the order into the two families of *Ustilaginaceæ* and *Tilletiaceæ*, and it shows how necessary it is for classificatory purposes to determine the mode of germination of the spore. There is general unanimity as to the division of the smuts into two families, but as to the limits of the genera there is difference of opinion. The one touches the other at so many points that there is always room for individual judgment in determining whether a genus shall be circumscribed or made to include a number of outlying forms, and what characters are to be regarded as essential.

Thus Cornu[1] has separated out from the genus *Ustilago* those forms which, instead of producing their spores more or less simultaneously, develop them in succession in spore-bearing hyphae arising from a so-called fertile stroma or persistent mycelium which surrounds a central columella, and for such species he has constituted the genus *Cintractia*. Wherever this feature is clearly shown of basipetal formation of the spores as in *C. axicola*, there, as a matter of convenience, the genus is adopted, although some would not consider it of sufficient importance to merit generic distinction.

Again, in addition to a central columella, there are some forms closely allied to Ustilago which are provided with a definite fungus membrane enclosing the spores, and which opens in various ways to allow them to escape. On account of this peculiarity, De Bary[3] has placed them in the genus *Sphacelotheca*, as illustrated in *S. hydropiperis*. But the fungus membrane enveloping the spores shows every gradation from that of *Sorosporium reilianum*, where it is partly composed of plant cells at the base of the ovary and entirely fungus cells at the top, to that of *Ustilago* (*Sphacelotheca*) *hydropiperis*, where the false membrane forms a special receptacle, splitting at the top to allow the escape of the spores. Besides, this membrane enclosing the spore-layer also occurs in species of Cintractia (*C. crus-galli*) and Sorosporium (*S. panici-miliacci*), so that the distinction is not sufficiently definite, in my opinion, to justify the formation of a new genus. Sometimes the plant tissues are hollowed out into cavities, and the simple spores develop there, thus constituting the monotypic genus *Melanopsichium*.

In such a genus as *Sorosporium*, where the spore-balls readily separate into their constituent spores, it is not always easy to separate it from Ustilago, especially when the mode of germination is the same. In order to be certain in some cases it is necessary to examine the spores in the early stages of their formation.

In *Thecaphora* and *Tolyposporium* the spore-balls are rather permanent, and it is mainly by the structure and germination of the spores that the difference is determined.

Just as in the family of the Ustilaginaceæ, the genus Ustilago is the starting point for a number of distinct genera, so in the family of the Tilletiaceæ there are clustered around the genus Tilletia a number of distinct types. While the spores are simple in *Tilletia*, they may unite to form permanent spore-balls as in *Urocystis*, the spore-balls consisting of an envelope of sterile cells surrounding one or several fertile spores. The spore masses, instead of being powdery and crumpent, may be permanently imbedded in the tissues. When the spores are simple and scattered through the substance of the tissues, this constitutes the genus *Entyloma*, but in some of the species the spores have a tendency to adhere irregularly in groups. This leads up to the spores being in balls as in *Doassansia*, where the spore-balls have a covering of sterile cells for the fertile spores.

The ten genera noted above are those which are definitely known to occur in Australia, but it will give us a wider outlook if we glance at the principal genera contained in the order as a whole. It is not so easy to settle what genera should be included in such a survey. A number have to be excluded, because they are now known to belong to other groups, and several have been proposed which are hardly sufficiently distinct from existing genera.

There are altogether nineteen genera, which may be arranged according to their outstanding features -whether the spores are single or in groups, whether exposed or imbedded in the tissues, whether the spore-balls are temporary or permanent, whether there are sterile cells at the centre or circumference of the ball, and finally the mode of formation of the spores and their germination.

USTILAGINACEÆ Tul.

Sori usually forming exposed powdery or agglutinated masses. Germination by means of a septate promycelium producing lateral and terminal conidia or sometimes by means of an elongated germinal tube without conidia.

I. Spores, single—

A. Sori powdery at maturity.

1. *Ustilago.*—Germination by 1–5 celled promycelium with lateral and terminal conidia, or sometimes developing directly into a mycelium.

B. Sori agglutinated at maturity.

a. Spores developed in a basipetal manner in hyphae arising from a persistent mycelium surrounding a central columella.

2. *Cintractia.*—Germination similar to that of Ustilago.

b. Spores formed in chambers inside the host-plant.

3. *Melanopsichium.*—Germination as in Ustilago.

I Spores chiefly in pairs—

A. Sori powdery.

a. Sori usually inside peduncles.

4. *Mykosyrinx.*—Germination not known.

B. Sori agglutinated.

a. Sori usually on leaves.

5. *Schizonella.*—Germination as in Ustilago.

III. Spores in balls—

A. Sori powdery.

a. Spore-balls rather temporary.

6. *Sorosporium.*—Germination by simple promycelium without conidia or by septate promycelium with lateral and terminal conidia.

b. Spore-balls permanent.

7. *Thecaphora.*—Germination by elongated septate promycelium only producing a single terminal conidium.

8. *Tolyposporium.*—Germination by septate promycelium with lateral and terminal conidia.

B. Sori agglutinated.

a. Spore-balls composed of spores with thick epispore.

9. *Tolyposporella.*—Germination by branched septate promycelium producing single lateral conidia.

b. Spore-balls with peripheral spores and central sterile cells.

10. *Testicularia.*—Spore-layer surrounded by a membrane of firmly united large round cells. Germination unknown.

TILLETIACEÆ Tul.

Sori forming powdery erumpent spore masses or permanently imbedded in the tissues.

Germination by means of a short promycelium, usually producing a terminal cluster of elongated conidia, which, with or without fusing in pairs, produce similar or dissimilar secondary conidia, or directly give rise to infection threads.

I. Spores, single—

A. Sori powdery at maturity.

a. Spores without conspicuous hyaline appendage.

11. *Tilletia.*—Germination by short promycelium with terminal cluster of elongated conidia, which, with or without fusing in pairs, produce a germ-tube.

b. Spores with elongated hyaline appendage.

12. *Neovossia.*—Germination as in Tilletia, and the conidia produce a germ-tube without fusing.

B. Sori permanently imbedded in the tissues.

a. Spores scattered in patches through the tissues.

13. *Entyloma.*—Germination similar to Tilletia, and often in addition tufts of conidia formed on protruding hyphae.

b. Spores in extended layers throughout the whole or portion of the plant.

14. *Melanotaenium.*—Germination by short stout promycelium, with terminal conidia not separating, but fusing in pairs.

II. Spores in balls—

A. Sori powdery.

a. Spore-balls with sterile peripheral cells.

15. *Urocystis.*—Germination as in Tilletia, or the terminal cluster of conidia produce directly long infection threads.

B. Sori permanently imbedded in tissues.

a. Spore-balls with sterile peripheral cells.

16. *Doassansia.*—Germination by a short promycelium, with terminal cluster of conidia, which often bear secondary and tertiary groups.

b. Spore-balls without sterile peripheral cells.

α. Spore-balls with or without central sterile parenchymatous cells.

17. *Burrillia.*—Germination as in Entyloma.

β. Spore-balls with central network of filaments.

18. *Tracya.*—Germination as in Doassansia.

γ. Spore-balls composed entirely of fertile spores which are dark coloured.

19. *Tuburcinia.*—Germination by promycelium with terminal conidia not separating, but fusing in pairs. Sometimes surface conidia produced from hyphae, forming conspicuous white growth.

CHAPTER XXIII.

Systematic Arrangement and Technical Descriptions.

Considering the wide distribution of the smuts and the numerous host-plants on which they grow, there is every reason to believe that there are still a number to be discovered in Australia. Apart from those which attack the cereals and which have consequently been brought prominently under notice, they have not attracted much attention, and it is only at particular seasons of the year that they are visible to the ordinary observer. Hence, while the following descriptions include all those which are at present known general conclusions cannot safely be drawn as to their distribution. Only the eastern portion of the Continent has received the attention of collectors, and the prevalence of smuts in the western portion is practically unknown. Much closer observation and extensive search is required before anything approaching a complete survey can be given, and if it be asked why then attempt it at all, I would reply that a clear and definite account of the forms already found will pave the way for further additions and discoveries. In some cases, too, there are only solitary specimens available, and the procuring of material at different stages and from various localities is desirable. The ten Australian genera have already been shown in their relation to genera in other parts of the world, and the 68 species have been described and illustrated in such a way that their identity can always be traced. It will be observed in the description of the species that I have used what is called the anatomical method, that is to say, the deep-seated characters as well as the more superficial ones, wherever possible.

Order—Ustilaginales.

Fungi parasitic in the tissues mainly of herbaceous flowering plants and developing a mycelium, local or widely extended, consisting of delicate, hyaline, septate, branching filaments, which often disappear partially or entirely at maturity through gelatinization and deliquescence.

Fertile mycelium composed of compact masses giving rise to spores from their internal contents, rarely forming conidia externally.

Sori evident, forming powdery or agglutinated masses of spores on definite portions of the host, sometimes permanently imbedded in the tissues.

Spores generally dark coloured, single, in pairs, or in spore-balls, which may be composed partly of sterile cells.

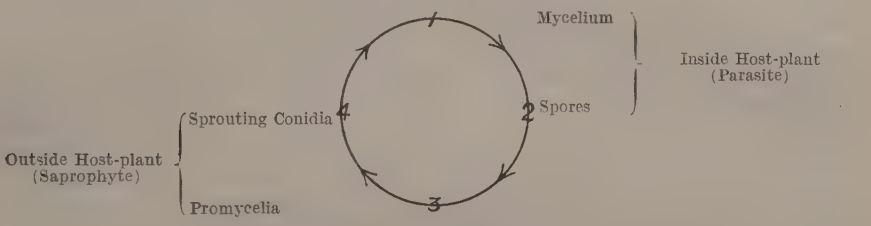
Germination by a promycelium, usually producing lateral or terminal conidia, which may either germinate in turn and directly penetrate the host-plant or reproduce themselves by budding in a yeast-like manner, and then germinating.

The Ustilaginales are typically parasitic fungi, which show the most perfect adaptation to their host-plants, and produce their spores asexually from single divisions or cells of the mycelium. But since parasites are assumed to have been derived from saprophytes, they still retain the saprophytic habit, and this is clearly seen, even in such pronounced parasites as the smuts.

When the spores escape from the host-plant, they can germinate readily in water, and produce a short germinal tube bearing single conidia, but in nutritive solutions they go further than this, and continue to produce reproductive bodies as long as the nutriment lasts. The spore germinates

outside the host-plant, and, as a rule, produces a germinal tube only once, but the conidia formed multiply indefinitely by direct sprouting or budding. This sprouting of the conidia in a yeast-like manner goes on until the nutriment is exhausted, and then they develop slender filaments, which, if they reach the host-plant at the proper stage, enter in and form the large septate spore-producing mycelia.

We have here the formation of different reproductive bodies inside and outside the host-plant. Inside a mycelium is produced, which finally gives rise to spores, and outside, the conidia, formed from the germination of the spore, sprout and multiply indefinitely. This continuous sprouting in a nutritive solution is the counterpart of the mycelium-forming spores confined to the host, and the germination of the conidia to form slender filaments in the exhausted solution is the connecting bridge between the outside and inside development. It may be represented graphically thus :—



While this is the general course of development, there may be slight deviations from it. In the American corn smut (*Ustilago zeae*) the sprouting conidia may not only occur in the fluid, but in the air, as aerial conidia. In Tilletia and other genera, not only is a whorl of conidia produced at the apex of the germinal tube, but the conidia may form in the air a mycelium like a tuft of mould, from which sickle-shaped aerial conidia again arise, singly and irregularly (Fig. 5). In Entyloma there is the further peculiarity that, in addition to the ordinary promycelial conidia, there are tufts of conidia produced on hyphae projecting from the host-plant itself.

It may finally be noted that infection through the flower, which is the only mode known in the loose smut of wheat and the naked smut of barley, is probably the most advanced form in which it occurs. The young ovary is not only attacked in its earliest stages, but the embryo itself is permeated by the fungus filaments, which are secure within the seed, and only await the germination of the seed to develop within the host-plant and produce its spores. The climax is reached in the Anther smut of the Carnation family, where the uncertain and wasteful dispersion of the spores by the wind is no longer relied on, but insects carry them from flower to flower as in the process of pollination.

The order may be grouped in two families, both of which are represented in Australia, and are distinguished by the mode of germination of the spores and the production of conidia.

Fam. 1. Ustilaginaceæ Tul.

This family is characterized by the spores germinating by means of a septate promycelium, which produces lateral and terminal conidia. The genus Ustilago, from which the family is named, is the richest in Australian species, and of the ten recognised genera, six of them have been found here, viz. :—Ustilago, Melanopsichium, Cintractia, Sorosporium, Thecaphora, and Tolyposporium.

Fam. 2. Tilletiaceæ Tul.

This family is named from the genus Tilletia, which comes next to Ustilago in the number of species. The spores produce on germination a short promycelium, which usually bears at its apex a cluster of elongated conidia. There are nine genera recognised, and only four are represented in Australia, viz. :—Tilletia, Entyloma, Urocystis, and Doassansia. Entyloma and Doassansia are distinguished by the spores being imbedded in the tissues.

USTILAGO Pers.

Vegetative mycelium spreading in the tissues of the host and soon disappearing.

Sori forming powdery, usually dark-coloured spore masses, on various parts of the hosts.

Spores single, small, produced irregularly in the interior of clustered terminal branches of fertile hyphae, which soon entirely disappear through gelatinization.

Germination by a short septate promycelium, which produces conidia both apically and laterally near the septa, or by a promycelium developing directly into a mycelium.

Conidia germinating in water, usually producing slender infection threads, but in nutritive solutions multiplying indefinitely after the manner of yeasts.

This genus contains the most species, and is the most important from an economic point of view. It includes some of the most destructive parasites of the cereals, and although it occurs on a great variety of hosts, the largest number are found on the Gramineæ. The only other host-plants represented here belong to the Cyperaceæ, Polygonaceæ, and Portulaceæ.

Brefeld divides this genus into three sub-genera or groups, according to the mode of germination, viz. :—Pro-ustilago, Hemi-ustilago, and Eu-ustilago ; but since the germination is not known in quite a number of Australian species this classification cannot be followed.

Australian species, 18.

Avena, Arrhenatherum.

1. **Ustilago avenae** (Pers.) Jens.

Jensen, Charb. Cereal, p. 4 (1889).
Brefeld, Unters. Gesammt., Myk. V., p. 54 (1883).
Brefeld, Unters. Gesammt. Myk. XI., p. 23 (1895).
Sacc. Syll. IX., p. 283 (1891).

Ustilago perennans Rostr.

Sori in spikelets, attacking all parts of the flower, even the glumes and awns, usually completely destroying the ears and transforming them into a dark-brown spore mass, which becomes powdery, and is eventually dissipated.

Spores globose to subglobose, occasionally ellipsoid, pallid to olivaceous or olive brown, more lightly coloured on one side, finely echinulate, 5½–6½ μ diam., or 7–8 × 5–6 μ, occasionally reaching an extreme length of 11 μ and a breadth of 7 μ.

On *Avena sativa* L.—Oats.

Common—wherever Oats are grown.

On *Avena fatua* L.—Wild Oats.

Victoria—Dookie, Nov., 1908. Longerenong, Nov., 1908.

On *Arrhenatherum avenaceum* Beauv. = *Avena elatior* L.—Oat grass.

Victoria—Longerenong, Nov., 1909. (Gibson.)

This smut is very common on cultivated oats, and occurs in all the States. It is usually confined to the inflorescence, but Clinton[4] records it as occurring on the leaves in rare cases, and Japp[1] found it in the anthers. It has been found on the wild oat in California, and occasionally on the same host in Victoria.*

Spore formation.—If cross-sections are made of an affected ovary in the young condition, the spores are seen forming around a central core of tissue, the youngest and colourless spores being innermost. They are also formed in isolated groups which may eventually run together. In these individual groups there is a Cintractia-like formation of spores, the very minute colourless spores being towards the centre, and the dark-coloured mature spores collected towards the circumference. The spores, however, are not agglutinated together to form that cheese-like consistency which is characteristic of Cintractia.

Germination.—Fresh material was taken from the field and the spores germinated freely both in water and nutritive solution. Germination takes place in a few hours, and a promycelium is produced, divided into segments by three or four transverse septa. Each of the segments generally bears a conidium, the top one producing it at the apex. The conidia may either fall away or remain attached, and give rise at their free end to a secondary conidium. The conidia when moist develop further, and may either directly put forth a slender germ-tube or two of them adjoining may become connected, and the one reinforced by the protoplasm of the other gives rise to a germ-tube. When spores are cultivated in a nutritive solution instead of water, an important difference arises. The conidia are formed as before, but they begin to sprout on their own account after the manner of yeast, and form sprouting conidia. In liquid manure this process of sprouting can go on indefinitely, and Brefeld maintained it over a year by keeping up the food supply. It must be remembered that this result was obtained with "pure cultures," but under natural conditions it is highly probable that the process would be checked, if not entirely hindered, by the development of other organisms. Spores have germinated after being kept for seven and a half years, and thus, in the staying power of the spores and in the immense numbers of sprouting conidia produced, this smut possesses unlimited powers of spreading.

(Plates VIII., IX., XXVI.)

Hordeum.

2. **Ustilago hordei** (Pers.) Kell. & Sw.

Kellerman and Swingle, Ann. Rep. Kans. Agr. Exp. Sta., p. 268 (1890).

Sacc. Syll. IX., p. 283 (1891).

Ustilago segetum (Bull.) Dittm.

U. jensenii Rostr.

Sori in spikelets, forming a black compact spore mass, enclosed in the glumes and covered rather permanently by the unbroken walls of the ovary, hence called covered smut of barley. Spores remain adherent, being bound together by patches of tissue in interior of spikelet.

* The wild oat can be infected with smut from the tame oat, and the tame oat with smut from the wild oat, so that the same species occurs on both. The form on the oat grass resembles the type in structure and germination, and the fact that the mycelium is perennial does not entitle it to specific distinction. Cross infection with the oat will be tried during the coming season.

Spores globose or subglobose to ellipsoid, olive-brown to blackish-brown, often with a clear strip on one side indicating a thinner portion of the wall, perfectly smooth, 6–9 μ diam. or 8–11 × 5–8 μ.

On *Hordeum vulgare* L.—Barley.

No doubt it occurs in all the States, although it has only been specially noticed as under :—

Victoria—Port Fairy, Dec., 1903, and Jan., 1905. Mordialloc, Sep., 1904. Camberwell, Nov., 1906. Toorak, Oct., 1907. Dookie, Dec., 1907. Goulburn Weir, Feb., 1909 (Parris). Bacchus Marsh, March, 1909.

Tasmania—Hobart, Dec., 1906 (Rodway).

South Australia—1907. Found in shipments of barley to Victoria.

In a shipment of wheat from San Francisco, arriving here in March, 1903, there were heads of barley and detached portions mixed up with it badly affected with this smut. Among the species of Ustilago on wheat, oats, and barley, there is not sufficient distinction in the size of the spores to discriminate between them, although the largest are found in *U. hordei.* It has also to be noted that it is the only one with a smooth epispore. The two species of smut found on cultivated barley—naked and covered smut—have only recently been separated, and they were formerly included under *U. segetum.* The hard and persistent mass of spores in the one case, however, and the powdery mass dispersed when mature in the other, enable them to be readily distinguished.

Spore formation.—A transverse section of the ovary shows the epidermis still surrounding it, and the spores are in patches scattered throughout the internal tissue. In each individual patch surrounded by plant tissue, when the spores are not all fully mature, they are seen to be formed in the sporogenous hyphae in regular gradation from the minute colourless to the mature coloured spore.

Germination.—Spores were germinated both in water and in hay infusion, and they put forth a germinal tube which divided by transverse septa into four cells, and conidia were produced laterally as well as at the apex. The conidia multiply in a yeast-like manner, and form sprouting conidia.

(Plates XI., XXVI., XXVII.)

Hordeum.

3. **Ustilago nuda** (Jens.) Kell. & Sw.

Kellerman & Swingle, Ann. Rep. Kans. Agr. Exp. Sta., p. 277 (1890).

Sacc. Syll. IX., p. 283 (1891).

Ustilago segetum (Bull.) Dittm.

Sori in spikelets, forming dense brownish-black masses, with a bronze-green tinge, at first covered by the flowering glume, which is converted entirely into a thin leaden-coloured membrane, or the awn may remain green, then when free from the leaf-sheath becoming naked, and the loosely adherent spores are scattered, leaving the axis of inflorescence exposed.

Spores globose to subglobose or ellipsoid, olive-brown, often with clear strip on one side, distinctly but finely echinulate, 5–7 μ diam., or 6–7 × 4–5 μ.

On *Hordeum vulgare* L.—Barley.

Very probably known in all the States, although not specially recorded.

Victoria—Port Fairy, Nov., 1890 (Pearson). Camberwell, Nov., 1906. Lindenow, Nov., 1906. Myrniong, Nov., 1906, and May, 1907 (Brittlebank). Burnley, Nov. and Dec., 1908.

This is known as naked barley smut, in contrast to the covered barley smut, under the life-history of which the chief differences have already been pointed out. It also appears earlier than the covered smut, and every ear is generally smutted in an infected plant.

A cross-section of the affected ovary is difficult to get, because the entire contents are ultimately replaced by spores, and even in the earlier stages only small patches of plant tissue remain.

Germination.—The spores germinate freely, both in water and nutritive solution. A septate germinal tube is produced which continues to grow at the apex and forms lateral branches, which in turn branch again, and so a spreading mycelium is developed without the formation of conidia. This absence of conidia is associated with infection taking place in the flower and not in the seedling, as is usually the case.

Treatment.—I have just received a Bulletin through the courtesy of one of the authors, E. M. Freeman, entitled *The Loose Smuts of Wheat and Barley*, in which a method of successfully treating this disease is given. Hitherto the only precaution known was to use healthy seed, since the mycelium of the fungus was inside, and could not be reached by the ordinary "steeps" used for other smut diseases. It has been found that Jensen's modified hot water treatment prevents both the loose smuts of barley and wheat, and the following method is recommended. "For barley, a soaking in cold water for five hours, followed by a soaking in hot water for fifteen minutes at a temperature of 52° C.; for wheat, a soaking in cold water for five hours, followed by a soaking in hot water for ten minutes at a temperature of 54° C. These treatments, if carefully carried out, entirely prevent the smut, and produce only slight injury to the germination of the seed.

"Thorough drying of the seed after the application of Jensen's modified hot water treatment is not injurious to the germination. When seed is injured by the treatment, the germination improves after several weeks of drying, and continues to improve for at least two months.

"The following method for farm practice is recommended:—Grow seed in a small isolated seed plot, using clean heavy seed of the best quality, and of pure stock. Treat this seed carefully by Jensen's modified hot water method as recommended, and sow the seed according to germination tests. Plant the seed from the seed plot the following year for the general farm crop. Maintain the seed plot every year."

(Plates X., XXVII.)

Triticum.

4. **Ustilago tritici** (Pers.) Jens.

Jensen, Ann. Rep. Kans. Agr. Exp. Sta. II., p. 262 (1890).
Sacc. Syll IX., p. 283 (1891)

Ustilago segetum (Bull.) Dittm.
Ustilago hordei Bref. (in part).
Ustilago tritici f. *folicola* P. Henn.

Sori in spikelets, attacking the glumes as well as the ovaries, forming dusty dark olivaceous masses, entirely destroying the floral parts as a rule, and leaving only the axis of inflorescence; occasionally on shot-blade forming elongated streaks, and also on rachis.

Spores pale olivaceous, more lightly coloured on one side, globose, subglobose, or shortly ellipsoid, minutely but distinctly echinulate, 5–6·5 μ diam., or 6–8 × 4–5·5 μ.

On *Triticum vulgare* Vill.—Wheat.

Common in all the States.

This is usually called Loose or Flying smut, from the way in which the spores are blown about, or "Snuffy Ears," from the dark dusty powder in place of the ear. The spores are blown about by the wind at flowering time, and by harvest time only the bare stalks of the affected ears are left, with remnants possibly of the chaffy scales.

It has been already noted that, while the spores are usually produced in the spikelets, they are occasionally found on the sheathing blade or shot blade, as well as on the stem (Plate VIc.). This only occurred on one variety, Red Egyptian, obtained from Vilmorin, of Paris, in 1908, and the elongated streaks were very prominent on both surfaces of the leaf. It is worthy of record in this connexion that Hennings[1] also found it on the leaves and leaf sheaths of a wheat obtained from Upper Egypt, and although the spores were identical, he regarded it as a new form, and named it *folicola*.

It sometimes happens that the spores remain closely agglutinated together, harden, and do not blow away, so that the axis of the inflorescence is invested by the black remains of the affected ovaries. A cross-section of such an ovary shows that the plant tissue has only been partially replaced by spores, and that, while the immature and colourless spores adjoin the vascular bundles, the dark dense mature masses are on the outside, the development of the spores being from the inside outwards.

Germination.—Both in water and in a nutritive solution, the spore puts forth a germinal tube which branches freely, and the tube with its branches curve in a characteristic sickle-shaped manner. No conidia are formed, but the whole grows into a much-branched mycelium. This species is adapted for floral infection, hence the mode of germination of the spore.

(Plates III., VI., XXVIII.)

Bromus.

5. **Ustilago bromivora** (Tul.) F. v. W.

Fischer von Waldheim, Bull. Soc. Nat. Mosc. XL., p. 252 (1867).
Cooke, Handb. Austr. Fung., p. 325 (1892).
Brefeld, Unters. Gesammt. Myk. V., p. 123 (1883).
Sacc. Syll. VII., p. 461 (1888).

Cintractia patagonica, Cooke & Mass. Grev. XVIII., p. 34 (1889).

Sori in spikelets, usually confined within the glumes, but sometimes attacking them at their base, at first bullate, then powdery, and the black spore powder frequently dusted over the entire inflorescence.

Spores dark-brown to olivaceous, globose to ellipsoid or ovoid, abundantly covered with minute tubercles, 7–10 μ diam., or 9–11 × 7–9 μ, occasionally 12 × 9 to 13 × 10 μ.

On *Bromus mollis* L.

Victoria—Common.

South Australia—Kangaroo Island, Jan., 1904 (Summers). Plains of Adelaide, Dec., 1909 (Quinn).

On *Bromus arenarius* Labill.

Victoria—Murray River (National Herbarium); Sea Lake, March, 1909.

On *Bromus unioloides* H. B. & K.—Prairie grass.

Victoria—Toorak, Melbourne, Dec., 1906. Domain, Melbourne, Dec., 1906 (Ewart). Narracan, Jan. and Feb., 1907. Horticultural Gardens, Burnley, Oct., 1907, to Oct., 1908, and to Oct., 1909. Murchison, Oct., 1907 (Wallace). Dookie, Dec., 1907. Coode Island, Nov., 1908 (C. French, jun.). Melbourne, Nov. and Dec., 1908 (C. French, jun.). Bairnsdale, Dec., 1908 (Smith). Burnley, Jan. to May, 1909. Myrniong, Feb., 1909. Treasury Gardens, Melbourne, Feb., 1909. Balwyn, Nov., 1909 (C. French, jun.). Willsmere, Dec., 1909 (Searle). Burnley, Dec., 1909, and Feb., 1910.

New South Wales—Singleton, Nov., 1903 (Cobb). Upper Hunter (Turner).

The smut has been found on the Prairie Grass all the year round. Usually all the spikelets of a panicle are infected, but I have found specimens in which the lowest spikelet bore sound seeds, while all the others were affected. In other cases the lower spikelets were affected and the upper clean (Fig. 15).

Spore formation.—A cross-section of the ovary shows dense dark-brown firmly agglutinated masses of spores arranged around various vascular bundles. The spores are seen radiating from these as a centre, at first colourless, and minute, and gradually increasing in size until they become mature and coloured.

The type of *Cintractia patagonica* on *Bromus unioloides* was examined by Clinton, and found to be this species. He regards it as an unusually vigorous form, because the basal parts of the outer glumes as well as the ovaries were infected, but this was a very common occurrence in our specimens.

The Cintractia type is suggested from the way in which the spores radiate from the various vascular bundles, but there is no central core of tissue from which the mass of spores radiates.

Germination.—The spore germinates freely in water, and I found it to retain its germinating power for at least two and a half years. It also germinates in nutritive solution, when the germinal tube is larger and more robust than in water. Brefeld[1] has shown that the conidia grow into bicellular sporophores, which sprout directly into new conidia.

(Plates XV., XXVIII.)

Agropyron.

6. **Ustilago bullata** Berk.

Berkeley in Fl. N. Zeal. II., p. 196 (1855).
Cooke, Handb. Austr. Fung., p. 326 (1892).
Brefeld, Unters. Gesammt. Myk. XII., p. 114 (1895).
Sacc. Syll. VII., p. 468 (1888).

Sori produced in the inflorescence and destroying it, at first enclosed in a greyish or leaden-coloured membrane which is soon ruptured, exposing the dark-brown to black compact mass of spores, sometimes only attacking portion of the spikelets.

Spores globose to subglobose or ellipsoid, olive-brown, densely warted, 8–11 μ diam., or 10–12 × 7–8 μ, occasionally reaching a length of 14 μ.

On *Agropyron scabrum* Beauv.

Victoria—Burnley, near Melbourne. Ardmona, Oct., 1895 (Robinson). Myrniong, 1900, Dec., 1901. Nov., 1904 and 1906, and Feb., 1909. Mt. Blackwood, Jan., 1903. Elmore, Apr., 1906. Rainbow and Lake Albacutya, Oct., 1908. Dookie, Dec., 1903 and 1907. Ardmona, Oct., 1909 (McLennan). Plenty Ranges, Nov., 1909 (C. French, jun.). Angustown, Dec., 1909.

Tasmania—Hobart, Feb., 1907 (Rodway).

South Australia—According to Cooke.

The membrane enveloping the sori consists mainly of the epidermal tissue of the plant.

I am indebted to the Director of the Royal Gardens, Kew, for specimens of this species collected by Colenso in New Zealand in 1849.

In the *Agricultural Gazette* of New South Wales a new species was described upon *Agropyron scabrum* as *U. agropyri*, but it was afterwards discovered that the material contained a mixture of Danthonia and Agropyron, and that it was really *U. readeri* Syd., which was there described as *U. agropyri* McAlp.

Spore formation.—A section of the ovary shows a central core of vascular tissue, sometimes very much reduced, with irregular outline and projecting processes. From the margin of this tissue the spores are developed, at first as minute colourless points, and gradually become coloured and mature. They radiate from the centre towards the circumference, where they form a continuous mass of olive-brown spores surrounded by the membrane. The membrane is ruptured, and the loose powdery spores escape.

Germination.—The spores germinate freely in water, and in about a couple of hours there were indications of the germ-tube. Brefeld[5] has described the germination from a specimen on *Agropyron orientale* Roem. and Schult. The spores germinated readily in water, but in a peculiar manner. Several germ-tubes were apparently produced from the spore at the same time, but all save one remained very short. This one elongated considerably forming transverse septa behind as the contents moved towards the apex. If the earliest stages of the germination are carefully observed, it will be seen how this arises. The germ-tube is originally simple and unbranched, consisting of three cells, of which only the lowest or rarely the two lowest grow out directly into long filaments, without the formation of conidia. With the outward growth of the lower cell the apex is turned to one side, so that at an early stage it gives the impression of three germ-tubes originating at the same time. If instead of water a nutritive solution is used, then it is quite different. A normal promycelium is formed, producing conidia, of which there was not even a trace in water. The single promycelium consisted of three cells, but when several were produced from the same spore, each was reduced to two cells. The elongated ellipsoid conidia sprouted even while still attached, but more luxuriantly when detached. The sprouting conidia were very slow in their growth, and inclined to form filaments before the nutritive solution was exhausted. In none of the cultures did fusions or aerial conidia occur.

(Plate XXIX.)

Calandrinia.

7. **Ustilago calandriniae** Clint.

Clinton, N. Amer. Ustil. Proc. Bost. Soc., p. 378 (1904).
Sacc. Syll. XVII., p. 472 (1905).

Sori in ovaries, at first of a deep dark-bluish tint, then purplish-black, pulverulent, without perceptible smell.

Spores globose, brownish-purple, 15–16 μ diam. epispore clear, reticulated, with ridges about 1.5 μ high and polygonal meshes about 2 μ diam.

On *Calandrinia calyptrata* Hook f.

Victoria—Minyip, Nov., 1897 and Oct., 1898 (Eckert). Rainbow, Oct, 1908. Murtoa, Nov., 1908 (Eckert). Myrniong, Dec., 1908, and Jan., 1909 (Brittlebank).

The spores are at first colourless and may sometimes remain so even when fully formed.

This smut does not prevent the host-plant reaching its full development, only the seeds are destroyed by it, and it attacks the plants growing in the same patch year after year.

This species was very abundant near Rainbow and wherever the plants occurred in patches, some of them were sure to be affected with the smut. It was only on close inspection that the smutted ovaries could be detected, as the same plant might bear flowers and fruits and smutted heads. The smutted ovaries were recognised by being more swollen than the healthy, even before bursting to allow the spores to escape.

Germination was tried in water with fresh spores and spores nine months old, but at first without success.

Germination.—This spore, although quite fresh, was somewhat difficult to germinate, and only after six days in distilled water. Only a few germinated in that time but they showed distinctly the formation of conidia as in Ustilago. The specimen from which the spores were taken was collected on 2nd January, and placed in germinating chamber on the 12th.

The spore may give rise to one (occasionally two) slender germ-tubes, straight or slightly bent, and sometimes forking at the end, reaching a length of 80–90 μ and up to 4-septate. The conidia are produced laterally and terminally, and are colourless and fusiform. Sometimes a conidium germinates while still attached, and produces a secondary conidium.

(Plates XXIX., LIII.)

Danthonia.

8. **Ustilago comburens** Ludw.

Ludwig, Zeitschr. Pflanzenkr. III., p. 139 (1893).
Sacc. Syll. XI., p. 231 (1895).

U. microspora Massee and Rodway, Kew Bull. p. 160 (1901).
U. exigua Sydow, Ann. Myc. I., p. 177 (1903).

Sori in upper portions of stem and in ovaries, ultimately destroying entire inflorescence and exposed on the rachis, covering it with a dense bronze-green powdery spore-mass, at first more or less compact.

Spores globose or ellipsoid, olivaceous in mass, clear yellowish-green individually, smooth, minute, 3–4·5 μ diam. or 4–4·5 × 2·5–3 μ, occasionally reaching 5·5 × 3·5 μ.

On *Danthonia pilosa* R. Br.

Victoria—Near Dimboola, Nov., 1892 (Reader). Kiewa, Nov., 1902 (Robinson). Kircheim, Oct., 1898 (Eckert). Lake Albacutya, Mallee, Oct., 1900 (C. French, jun.). Rainbow, Oct., 1908. Mallee, Nov., 1903 (Williamson Wallace).

Tasmania—Risdon, near Hobart, May, 1899 (Rodway).

On *Danthonia* sp.

South Australia—Murray Bridge, Dec., 1892 (Tepper).

Dr. Ludwig has kindly sent me a portion of the original material which is given as occurring on *Stipa*, but on comparing both the host and the fungus with that found on *Danthonia*, it is seen to be the same, and that the host-plant has been wrongly determined.

In Dr. Cooke's Australian Handbook this species on *Danthonia* is given as *U. segetum* Bull.

This species was first named by Dr. Ludwig in 1893 from specimens sent by Mr. Tepper. Then Massee received a specimen from Rodway later and it was named *U. microspora*, but since the name was pre-occupied by Schroeter and Henning in 1896, it was changed to *U. exigua* by Sydow. However, the original name of Ludwig now stands.

Spore formation.—Cross sections of the stem show the various tissues of the host-plant, and the fibro-vascular bundles are penetrated by the mycelium. On the outside of the outer ring of bundles a continuous stroma or compact mass of filaments is formed, and the projecting hyphae develop spores in succession. The inner are colourless, but towards the outside they become olivaceous and are held together at first by the remnants of the stroma. All the hyphae arising from the stroma seem to become spore-bearing, and detached portions of the outer tissues occur among them.

Germination of 1902 material was tried several times but did not succeed. Spores collected in October 1908 were placed in a Petri-dish with water on 21st January, 1909. It was only after nine days that they began to germinate, and produced occasionally a one-septate promycelium about 6 μ long.

(Plates XIX., XXXVII.)

Panicum.

9. **Ustilago confusa** Mass.

Massee, Grev. XX., p. 65 (1892).
Cooke, Handb. Austr. Fung., p. 324 (1892).
Sacc. Syll. XI., p. 230 (1895).

Sori in ovaries, soon naked, pulverulent, violet-black.

Spores clear-brown, with a tinge of violet by transmitted light, subglobose or irregularly angular, epispore about 1 μ thick, perfectly smooth, 11–12 μ diam.

On *Panicum paradoxum* R. Br. = *Chamaeraphis paradoxa* Poir.
Victoria.

It was previously confounded with *Ustilago destruens* Schlecht, from which it is distinct.

Specimen not seen, and informed that there is no material available at the Royal Gardens, Kew. Whether this species agrees with others recorded on species of Panicum can only be settled when the smut is again discovered on this host-plant.

Cynodon.

10. **Ustilago cynodontis** P. Henn.

P. Hennings, Engl. Bot. Jahrb. XIV., p. 369 (1891).
Sacc. Syll. XIV., p. 416 (1899).

Sori involving the young inflorescence and entirely destroying it while still enclosed in its enveloping leaves, black in the mass and powdery; in some cases the digitate spikes have expanded before the florets are destroyed; also in the axis of the inflorescence and encircling it.

Spores olivaceous, subglobose, occasionally ellipsoid, almost smooth, 7–8 μ diam. or 9–10 × 5–7 μ.

On *Cynodon dactylon* Pers.—Couch grass.

New South Wales—Sydney Botanic Gardens, Jan. and Oct., 1907 (Cheel). Sydney, Feb., 1909 (Baker).

This species was first obtained from Abyssinia, then it was sent from Simla in 1891 to Brefeld, who succeeded in germinating the spores. Magnus[4] notes its distribution in Europe, Northern Africa, and India, and concludes that the Ustilago on the same host-plant in America is quite distinct.

In Australia it has only hitherto been found in the Sydney Botanic Gardens and on a lawn near Sydney. Although the host-plant is plentiful in Victoria, no signs of smut have appeared on it.

Spore-formation.—Cross-sections of the stem and of the axis of the affected inflorescence show the plant tissues in the centre surrounded by the vascular bundles, and the hyphae are seen ramifying in the cells outside these bundles. The mycelium bursts through the epidermis and forms a compact mass of filaments from which the spore-bearing hyphae are produced. The very minute colourless spores are at the base, and they gradually increase in size and assume a dark olivaceous tint towards the outside. Here and there are slender strands of hyphae radiating towards the circumference and if the spores were more firmly agglutinated together, the characters would be those of a Cintractia.

Germination.—This occurred in water, and in a nutrient solution every spore germinated. Spores were taken from a specimen collected in October, 1907, and in December, 1908, they germinated freely, thus showing that they retain their germinating power for more than a year. The spore puts forth a three-celled promycelium which produces elongated conidia laterally and at the apex. In some cases two promycelia are produced from one spore, the spore itself being divided into two by a septum and each division giving rise to a promycelium. The conidia multiply copiously by sprouting, and these *sprouting* conidia, where they reach the surface of the fluid, become *aerial conidia.*

(Plates XXII., XXXIV., LIII.)

Triodia.

11. **Ustilago hieronymi** Schroet.

Schroeter, Hedw. XXXV., p. 213 (1896).
Clinton, North Am. Ust., p. 358 (1904).
Sacc. Syll., XIV., p. 417 (1899).

Sori in the leaves and leaf-sheaths, usually forming elongated pustules covered by the leaden-coloured cuticle which usually ruptures, exposing the mass of powdery black spores.

Spores dark-brown, globose to ellipsoid, distinctly warted, 10–12 μ diam. or 10–13 × 7–10 μ, occasionally reaching a length of 15 μ.

On *Triodia mitchelli* Benth.

Queensland—(Bailey).

Bailey kindly sent me a specimen from his Herbarium, and in an accompanying note remarked— "I obtained it many years ago and sent samples to Berkeley and Broome, who at first named it *Ustilago carbo* Tul., afterwards changing it to *U. segetum* Berk.

In the original description of this species on *Bouteloua ciliata* Grisel. from the Argentine, the spores are given as 11–15 × 8–13 μ and said to be somewhat punctate. Clinton also records it on *Triodia pulchella* H. B. and K. from Arizona, and speaks of the spores as rather obscurely echinulate, but in the Queensland specimens they are prominently so.

This is a very variable species, and in the absence of sufficient material on Triodia for fuller investigation, this particular smut will be retained here for the present.

(Plate XXXI.)

Polygonum.

12. **Ustilago hydropiperis** var. **columellifera** Tul.

Berkeley, Journ. Linn. Soc. London XIII., p. 174 (1872).
Cooke, Handb. Austr. Fung. p. 327 (1892).

Sori produced in the ovaries, the solitary ovule of each being completely transformed and replaced by the fungus; the outer portion sharply defined and compact; composed of spore-like barren cells, forms a distinct urn-shaped spore-receptacle, open at the top and with reflected margin, the central portion projects as a dark-purplish body, the so-called columella, up to 4 mm. long, hollow in the centre, composed of similar cells to that of the wall, and coated with a dense mass of the violet-coloured spores.

Spores purplish, oblong to ovoid, but generally subspherical, very finely echinulate, 10–13 μ diam. or 11–12 × 8 μ.

On *Polygonum minus* Huds.

Tasmania—Near Launceston, March, 1893 (Rodway).

On *Polygonum* sp.

Queensland—(Bailey).

In the transverse section of this fungus (Pl. XXXII.) towards the base of an affected ovary, the wall of the ovary is seen detached quite unaffected by the fungus. Inside, the tissue of the ovule has been entirely replaced by fungus cells, the centre being hollow. The inner colourless cells surrounding the cavity are similar to those on the outer side, and the dark-purple ring between consists of the spores. The colourless cells readily separate from each other and are subspherical, differing from the spores in having generally a thicker wall, which is not echinulate. The spores gradually merge into them on either side, and they are, in all probability, immature spores. When fully developed, the outer wall splits at the top, forming an urn-shaped receptacle, while the central portion elongates as the columella carrying some of the spores with it.

The species of which the above is considered a variety was made the type of a new genus by De Bary, and named by him *Sphacelotheca* mainly on account of the distinct spore-receptacle formed of fungus cells, but also because of the central columella and the differentiation of the spore-layer into sterile

and fertile cells. The development of this species, as described by De Bary, will show so clearly the nature and origin of the different parts that it will be given briefly before discussing the necessity for a new genus.

When the ovule is fully formed, the hyphae pass through the flower-stalk into the ovary and reach the ovule through its funicle or stalk. There the parasite penetrates the tissue to such an extent that the ovule is replaced by a compact mass of densely interwoven hyphae with gelatinous walls. The fungus is confined entirely to the ovule, and becomes differentiated into a thick colourless outer wall, a central axile cylinder or *columella*, and between the two a dense mass of violet-coloured *spores*. The base of the ovule remains undifferentiated, and there new hyphae are constantly being formed which add to the height of the parts already formed and consequently give them a cylindrical form.

The fully-formed wall consists of several layers of minute round cells, similar in size to the spores and produced in the same way from the hyphae of the primary tissue, but with a colourless membrane. The columella has generally the structure of the wall, and the spores are developed around the columella in a dense ring about equidistant from the centre and circumference. The wall of the ovary is not attacked by the fungus, and does not follow the growth of the spore-receptacle so that it is soon ruptured. The wall of the spore-receptacle itself is very fragile and readily bursts at the top to allow the escape of the spores. The development and germination of the spores are the same as in Ustilago, the compact mass of much-branched spore-bearing filaments having gelatinous walls as in that genus.

It will be seen from this description that the species differs considerably from that of any other Ustilago, particularly in the distinct spore-receptacle made up of fungus cells, but there are various gradations in the formation of a fungus membrane enclosing the spores in different species, and the difficulty is where to draw the line. The presence of a central columella is also not uncommon, although it is often composed chiefly of the plant-tissues, and the differentiation of similarly produced cells into colourless sterile cells, and coloured fertile cells is found in various other species of Ustilago, such as *U. cruenta*, Cintractia as *C. leucoderma*, and Sorosporium as *S. panici-miliacei*, so that the presence of a fungus membrane enclosing the spores cannot be regarded as of generic value. While there is a general resemblance in this variety to the type species which has already been recorded on *Polygonum minus* in other parts of the world, yet there is sufficient distinction, perhaps, to make it worthy of being classed as a variety. The cylindrical projecting columella is very characteristic, and, on comparing the spores with those from *U. hydropiperis* in Rab. Fung. Eur. No. 2601, they are slightly smaller.

(Plate XXXII.)

Carex.

13. **Ustilago olivacea** (DC.) Tul.

Tulasne, Ann. Sci. Nat. Bot. III., Vol. VII., p. 88 (1847).
Brefeld, Unters. Gesammt. Myk. V., p. 129 (1883).
Sacc. Syll. VII., p. 463 (1888).

Ustilago catenata Ludwig, Zeitschr. Pflanzenkr. III., p. 139 (1893).

Sori only produced in some of the ovaries of the inflorescence, often more or less concealed at first by the perigynium; olive-brown spore-masses, firmly agglutinated at first; finally more or less powdery and intermixed with conspicuous filaments.

Spores olive-brown, variable in size and shape, often arranged in chain-like rows and accompanied by long hyaline filaments, subspherical to ellipsoid or oblong to linear, densely warted, 6–7 μ diam. when subspherical, and 7–13 × 4–6½ μ when elongated.

In spikes of *Carex pseudo-cyperus* L.

Tasmania—Huon, Dec., 1894 (Rodway).

South Australia—Mount Lofty Range, 1893 (Tepper).

A specimen was sent to Ludwig from South Australia by Tepper on a host-plant supposed to be *Cyperus lucidus* R. Br. He determined the smut as a new species (*U. catenata*) but recognised it as being closely allied to *U. olivacea*. Ludwig kindly forwarded me some of the original material, and it was evidently the same as *U. olivacea*, but I presume Ludwig was mainly influenced in making it a new species from being found apparently on a different genus of host-plant. On submitting the plant to L. Rodway, F.L.S., he determined it as unmistakably *Carex pseudo-cyperus*, so that I have made Ludwig's species a synonym.

Spegazzoni had already recorded it on this species from the Argentine Republic, but Saccardo made it a variety—*pseudocyperi*—on account of the spores being 6–12 × 6–10 μ. We found no spores as broad as this, and have retained the original species. This smut is confined to species of Carex and chiefly those which grow under damp conditions. Only a few of the ovaries of a spike are affected, but the rain readily spreads the spores over the parts beneath. It is easily recognised, not only from the olivaceous tint overspreading the spike, but from the tufts of filaments which project from the ovaries which are attacked, and it is this peculiarity chiefly which has attracted a considerable amount of attention to this species. Among the irregularly twisted web of filaments there are two kinds to be distinguished—those which produce the spores and those which remain barren. The spore-producing filaments show the formation of spores at various stages. At first the filaments exhibit swellings quite close to one another, like a string of beads or a series of knots, then cross-partitions are formed separating each swelling, the contents of which becomes a spore.

There are other filaments, however, which are sterile and do not form spores, but are mixed up with the spores like the filaments composing the capillitium in the Puff-balls. How these filaments originate and what is their function has not been explained, but probably they serve in some way to scatter the spores over a wide area.

The characteristic elongated spores are usually found in chains from the mode of their formation.

Germination.—This has been determined by Brefeld[1] both in water and in a nutritive solution. The spores germinate readily in water after a few hours, putting forth an exceedingly fine germinal tube, which elongates and then becomes detached as a conidium. In the case of small spores this completed the germination, but with large spores a second conidium is formed. The detached germinal tube gave rise to a secondary conidium and ended there. In a nutrient solution the spore germinated as before, only giving rise to a succession of conidia, each of which when detached produced a secondary conidium, or several might remain attached to the spore and bud, but large colonies were never formed. It will be seen from this description that there is, strictly speaking, no germinal tube, it is unicellular and does not differ from the conidium directly proceeding from it. Hence the only means of multiplication is by sprouting conidia.

(Plate XXIX.)

Setaria.

14. **Ustilago pertusa** Tr. and Earle.

Tracy and Earle, Bull. Torr. Bot. Club, p. 175 (1895).
Sacc. Syll. XIV., p. 415 (1899).

Sori in ovaries, hard, compact, black, finally pulvinate.

Spores small, globose, brownish, epispore covered with prominent irregular spikes, very constant in size, 5–6 μ diam.

On *Setaria macrostachya* H. B. and K.

Queensland—1890 (Bailey).

In the original description, the host is given as *S. macrochaeta*, but this is evidently a misprint, as this grass does not occur in Australia.

In *U. viridis* Ell. and Ev. the spores are slightly smaller, and form a yellowish-green coat on the outside of the seeds.

Danthonia.

15. **Ustilago readeri** Sydow (in letter 1905).

Ustilago agropyri McAlp. Agr. Gaz. New South Wales, p. 154 (1896).

Sori in stems, leaves, and ovaries, black, pulverulent, usually destroying entire inflorescence, at first enclosed by the leaf-sheaths when in ovaries, ultimately exposed and the spores dissipated, leaving the rachis bare or with the glumes still attached.

Spores dark-brown, globose to ellipsoid, apparently smooth but delicately echinulate, 10–13 μ diam. or 11–14 × 8–11 μ.

On *Danthonia penicillata* F. v. M.—Wallaby grass.

Victoria—Burnley and Ardmona, Oct., 1892 (Robinson). Dimboola, Nov., 1892 (Reader). Myrniong, Dec., 1900 and 1908 (Brittlebank). Kergunyah and Killara, Nov., 1902 (Robinson). Casterton, Dec., 1905 (Reader). Darebin Creek, Oct., 1906 (C. French, jun.). Cheltenham, Oct., 1906 (Robinson). Emerald, Nov., 1906 (McLennan). Camberwell, Dec., 1907, Oct. and Nov., 1908 (C. French, jun.). Rainbow, Oct., 1908. Plenty Ranges, Nov., 1909 (C. French, jun.). Angustown, Dec., 1909.

New South Wales—Penshurst, Nov., 1908 (Cheel).

South Australia—Port Elliot, Nov., 1901 (Summers). Blumberg, Nov., 1904 (Tepper).

Tasmania—Huon River, Jan., 1903 (Rodway). Hobart, Jan., 1906 (Rodway). Devonport, Jan., 1906 (Robinson).

On *Danthonia* sp.

Victoria—Caromby, Oct., 1889 (Tepper). Whittlesea Ranges, Nov., 1898 (C. French, jun.)

U. danthoniae Kalch. is quite distinct since the spores are given as 36 μ diam.

This smut is not at all uncommon on Danthonia, attacking the leaves and stems as well as the inflorescence, and it has, unfortunately, received a variety of names. The earliest specimen, found in Victoria in 1889, was sent through Tepper to Professor Saccardo[2], who determined it as *Ustilago leucoderma* Berk. Berkeley's species was characterized by being clothed externally with a white rugged crust, and was afterwards found to be a Cintractia and named *C. leucoderma* (Berk.) P. Henn.[1] It has been found on *Rynchospora aurea* Vahl. in Victoria, but it is quite distinct from the smut on Danthonia.

Then in 1892 Massee determined a specimen sent from Victoria by Reader on *Danthonia penicillata* as *Ustilago destruens* Schlecht., and the same species had been previously recorded on Danthonia by Cooke[3]. Finally, in 1896[4], I described what was really the present species under the name of *U. agropyri*, as there was a mixture of material of Agropyron and Danthonia which was afterwards separated out.

It simply remains now to compare this species with that of *U. destruens* Schlecht. = *U. panici-miliacei* (Pers.) Wint. = *Sorosporium panici-miliacei* (Pers.) Takahashi.

As Takahashi[1] has clearly shown the species referred to by Massee is a Sorosporium and not an Ustilago, the spore-balls being rather evanescent at maturity. The smut pustules are covered by the epidermis of the host with a layer of sterile hyphae in close contact and fibro-vascular bundles traverse the pustule together with hyphal strands.

The external appearance as well as sections of *U. readeri* clearly show how distinct this species is. On the stem it forms elongated blister-like swellings, and the leaden-coloured epidermis soon ruptures to allow the escape of the spores. It sometimes completely surrounds the stem which is longitudinally furrowed as the swollen epidermis bursts and exposes the spores.

A cross-section of the stem shows the hollow cavity in the centre, and in the plant tissue immediately beneath the epidermis scattered patches of spores are developed. Sometimes these isolated patches blend here and there and form a larger one, and finally the epidermis is elevated and ruptured to allow of the escape of the spores.

A cross-section of the axis of inflorescence shows the central core of plant tissue either solid or with a small cavity, and surrounding that the patches of spores are developed, so numerous and so close together, that they ultimately form a dense continuous mass, covered by the epidermis until it is ruptured.

A cross-section of the ovary shows the central vascular bundles completely surrounded by dense masses of spores. The spore-forming hyphae have evidently penetrated the larger vessels as they are seen to be filled with spores at different stages of development, and finally the entire tissue of the ovary would be replaced by spores.

Germination.—The spores germinated readily in water and also very luxuriantly in Cohn's modified solution. Fresh spores and spores one year old readily germinate, but when the material is two years old only an occasional spore germinates. It is one of the easiest spores to germinate, and if not too old can always be relied upon to do so in a few hours. Spores taken from *Danthonia penicillata* F. v. M., collected in December, 1905, germinated in July, 1906, and also in December of the same year. The germinating spores figured (Pl. LIII., Figs. 203, 204, 205) are from *Danthonia penicillata* collected in December, 1908, and they were germinated at once.

The spores when germinated in water put forth in a few hours a straight promycelium which at first is non-septate (Pl. LIII., Fig. 203). Then it elongates and becomes divided by several septa, when it may either produce conidia (Pl. LIII., Fig. 204) or elongate further (Pl. LIII., Fig. 205). The conidia are produced laterally and terminally, only a few lateral and one apical. They are colourless, cylindrical, rounded at the ends, 6–9 μ long, and may or may not be attached by a short sterigma. Only occasionally one produces another by budding while still attached. The promycelium, however, may and often does forego the formation of conidia. It grows out at the apex of the septate portion or

laterally or even direct from the spore as a slender, elongated, more or less wavy filament, which may reach a length of 200–300 μ. At first it is non-septate, but afterwards becomes septate and even branched. The spore may give rise to two promycelia, one being usually shorter than the other.

Spores immersed in liquid do not germinate as readily as those floating on the surface. Thus, after 18 hours on one occasion, the spores in the water had failed to germinate, while by simply altering the focus and examining the spores on the surface, they were all found, with very few exceptions, to have germinated. This germination at the surface was in various stages. Some had just put forth a short, slender, simple promycelium; others had produced an elongated, septate promycelium; and still others had put forth slender branches from the segments of the promycelium. In some cases the septate promycelium tapered out into a long wavy filament, and when the liquid began to dry up, these filaments became exceedingly long and exceedingly wavy, and ultimately became detached.

(Plates XVIII., XXXI., LIII.)

Stenotaphrum.

16. **Ustilago stenotaphri** McAlp.

McAlpine, Agr. Gaz., New South Wales, Vol. VI., p. 758 (1895). Sacc. Syll. XIV., p. 415 (1899).

Sori on stem and leaves, giving them a blackened appearance as if charred, compact, completely surrounding part attacked, which is usually the younger growth.

Spores dark-brown, subglobose to ellipsoid or irregular, smooth, 16–17 × 10–13 μ.

On *Stenotaphrum glabrum* Trin. (Buffalo grass) = *S. americanum* Schrank.

Victoria—Kew, June, 1890 (Ralph).

There is another smut affecting Buffalo-grass, but it occurs in the spikelets, and the spores are only 5–9 μ in length. This is *U. affinis* Ell. and Ev., but it was also named *U. stenotaphri* by P. Hennings (1898) and Massee (1899) respectively. The host-plant is frequently regarded as an introduced grass, but it is a true native of Australia, as well as of America.

(Plate XXXII.)

Amphipogon, Neurachne.

17. **Ustilago tepperi** Ludw.

Ludwig, Bot. Centr. 341 (1889).

Sori in stem and flowers, black, powdery, destroying the parts affected. Spores globose or shortly ellipsoid, brown, papillate or rather aculeate, 12–17 μ diam.

On *Amphipogon strictus* R. Br. and *Neurachne alopecuroides* R. Br.

South Australia—Torrens Gorge and Highbury Scrub (Tepper).

I could not obtain a specimen of this smut, and have never met with a smut of any kind on either of these hosts.

18. **Ustilago utriculosa** (Nees) Tul.

Tulasne, Ann. Sci. Nat. Bot. III., p. 102 (1847).
Cooke, Handb. Austr. Fung., p. 326 (1892).
Brefeld, Unters. Gesammt. Myk. XII., p. 139 (1895).
Sacc. Syll. VII., p. 476, (1888).

Sori inside floral envelopes, causing the blossoms to become swollen, dark-violet to purplish, powdery.

Spores globose or subglobose, occasionally ellipsoid, transparent, violet, reticulated with very high ridges which form meshes 2–3 μ wide, 10–13 μ diam. or 11–13 × 8–11 μ.

On *Polygonum minus* Huds.

Victoria—Near Melbourne, June, 1884 (Reader). Tambo River, Feb. (National Herbarium). Casterton, Dec., 1908 (Reader).

Queensland—(Bailey, No. 59).

On *Polygonum prostratum*, R. Br.
Victoria—Dimboola, March, 1898 (Reader).

On *Polygonum hydropiper* L.
Victoria—Tinandra, May, 1909 (Whittekers).

The Queensland specimen was labelled *Sphacelotheca hydropiperis*. The swelling of the ovaries and the dark purple spore-masses are very characteristic.

Spore formation.—A cross-section of the ovary shows that the spores originate from hyphae adjoining the vascular bundles, where they are seen as minute colourless specks, gradually acquiring a round form and a netted epispore, with the development of a violet colouration.

Germination.—This has been described and illustrated by Brefeld[5]. The spores do not germinate, as a rule, in the autumn when they are formed, but in the following summer, after lying on damp earth. In water they produce a triseptate promycelium, which soon gives rise to lateral and terminal elliptical conidia. These become detached and again produce smaller conidia without further development. In a nutritive solution, there is a more luxuriant formation of conidia, with unlimited capacity for sprouting in a yeast-like manner. Neither fusion of the conidia nor their germination has been observed.

Spores from a specimen of *Polygonum hydropiper* L., obtained in May, were placed in tap water towards the end of September. In two days they germinated freely, and in three days the great majority had germinated. The promycelium was generally three septate, 3–4 μ broad, and branches were frequently produced beneath the septa, the terminal segment often giving rise to a slender elongated filament. Conidia were produced both laterally and terminally, but the formation of branches from the segments of the promycelium was more common. They generally arose from the basal and terminal segments and reached a length of 60 μ, while the promycelium itself was only 16 μ on an average.

(Plate XXXII.)

MELANOPSICHIUM Beck.

Mycelium intermixed with the diseased plant tissues, which are hollowed out into cavities, containing the spore-bearing gelatinous hyphae.

Sori on various parts of the host, forming compact, hard, conspicuous, gall-like masses, black when cut across, and the galls consisting of a mixture of plant tissue and hyphae.

Spores single, as in Ustilago, and germination similar, developed in cavities of various shapes and sizes, which are sometimes confluent.

There is only a single species of this genus known, which was formerly placed under Ustilago. It was originally found in South America and now in the United States and Australia. The development of the spores in cavities, the walls of which consist of the plant tissues and the mycelium intermixed, is the characteristic feature of the genus.

Australian species, 1.

Polygonum.

19. **Melanopsichium austro-americanum** (Speg.) Beck.

Beck, Ann. K. K. Natur. Hofmus. Wien, p. 22 (1894).
Sacc. Syll. VII., p. 457 (1888).

Ustilago austro-americana Speg. Fung. Argent., pug. 4, No. 45 (1881)

Forming compact, hard, rough, lobed, oblong, ruddy-brown galls around joints of stem, up to 1 cm. in size, black when cut across.

The gall consists of the various tissues of the stem—epidermis, cortex, and fibro-vascular bundles—for the most part hollowed out into cavities which are the sori.

Sori of various shapes and sizes, generally marked off by definite tissue, round to oval or oblong, adjoining one another and sometimes confluent; ranging from 70 μ long when young up to 500 μ or more when mature.

Spores olivaceous, ellipsoid to ovate, prominently echinulate, 10–14 × 7–8 μ.

On *Polygonum* sp.

Queensland—Near Brisbane, April, 1879 (Bancroft).

The spores are developed in gelatinous hyphae which deliquesce and set free the spores in the cavity. As the sori are completely surrounded by the outer tissues of the stem, the spores can only escape by the decay of the tissue, or by the absorption of water and the oozing out of the ripe spores. Only a single species of this genus has, so far, been known, and although in the United States specimens the sori were chiefly in the inflorescence, and in South America, where it was first found, chiefly on the leaves, yet the general characters of this specimen agree so well with the type, that I have no hesitation in referring it to the same species. A specimen examined from Clinton's Ustilagineæ C. 35, on *Polygonum lapathifolium* had the same characters.

This Queensland specimen was given by Cooke in his *Handbook of Australian Fungi* as *Ustilago emodensis* Berk.

Berkeley founded this species on a single specimen from Tonglo, in the Sikkim Himalaya, 10,000 feet high, and he described it as forming a lobed tubercle; spores ovate or elliptic, deep lilac, smooth, very minute, traversed

by radiating forking threads. Then Cooke supplemented this description later by giving the size of the spores as 12–15 μ diam. and their surface is described as delicately rugulose. There is no trace of lilac in the spores of the Queensland specimen, which is, however, at least a quarter of a century old, nor of the bifurcating filaments.

The original determination of this species as *Ustilago emodensis* Berk. was made by Mr. Broome, as the following note from Mr. Bailey will show :— "My only specimen of *Ustilago emodensis* was given to me by the late Dr. Joseph Bancroft, who found it on *Polygonum* sp. at Kelvin Grove, Three-mile Scrub near Brisbane, April, 1879. It was determined by the late Mr. Broome."

Massee[6] has made *Ustilago treubii* Solms. a synonym of *U. emodensis* Berk., but it has certainly no relation to the Queensland specimen. Dr. Treub kindly sent me specimens from Java on *Polygonum chinense*, and they show the clustered outgrowths, up to 1 inch long, forming a swollen head like a *Cantharellus*. The swollen head splits across and allows the escape of the violet-tinted spores, which are globose to ellipsoid, very delicately echinulate and 7–8 μ diam. or 7–8 × 5–6 μ. Dietel[1] describes them as smooth and only 4 μ diam. The arrangement of the spores and their size and colour are altogether different to those of Melanopsichium.

On forwarding photographs of *Melanopsichium austro-americanum* and *Ustilago treubii* to the director of the Royal Gardens, Kew, he courteously replied—"that an examination of the original specimen of *Ustilago emodensis* Berk. had been made. The plant proves to be very different from Bailey's Queensland plant, having spores irregularly globose, violet, thick-walled, almost smooth, and measuring 5–7 μ diam. *Ustilago treubii* Solms. (Exsicc. No. 56) has also been examined and it is, as stated by Mr. Massee, practically identical with Berkeley's species."

Germination.—This has been described and figured by Norton[2]. He says— "It begins in water after a day or two and proceeds slowly. The promycelia are small and slender, frequently branched, and irregular in shape. Conidia few."

(Plate XXXIII.)

CINTRACTIA Cornu.

Mycelium usually persistent in the diseased parts, with a compact gelatinous base from which spore-bearing filaments arise, in which the spores are successively differentiated from the inside outwards.

Sori on various parts of the host, forming a compact usually firmly agglutinated spore-mass, generally surrounding a central columella of plant tissue.

Spores single, as in Ustilago, and germination the same, or only slightly modified.

This genus was named by Cornu after a distinguished French botanist called Cintract. It is not always recognised as distinct from Ustilago, but the distinction lies in the spores remaining firmly agglutinated and compact for a considerable time, while the spores themselves are developed successively from a fertile stroma. Eventually they are generally freed by the absorption of water, as the host-plants usually occur in damp situations and the moisture at the same time insures germination. The hyphae arising from

the gelatinous base may be entirely spore-bearing, or there may be strands of undifferentiated hyphae, between which the fertile hyphae produce masses or pockets of spores.

The characteristic features of Cintractia are the central columella of plant tissue, the development of spores from the inside outwards, and the firmly agglutinated spores. As might be anticipated, there are some cases where it is difficult to say whether the species should be regarded as an Ustilago or a Cintractia, as in *Ustilago avenae*, for instance, where there are only the powdery spores to separate it from Cintractia, but if the three characters given above are observed, then the genus will be a very convenient one.

Australian species 11.

Fimbristylis.

20. **Cintractia axicola** (Berk.) Cornu.

Cornu, Ann. Sci. Nat. Bot. p. 279 (1883).
Cooke, Handb. Austr. Fung., p. 324 (1892).
Sacc. Syll. VII., p. 480 (1888).

Ustilago axicola Berk., Ann. Nat. Hist., p. 200 (1852).
Ustilago fimbristylis Thuem., Bull. Torr. Bot. Club, VI., p. 95 (1875).

Sori usually at base of flower stalks, forming compact, black, roundish swellings, at first covered with whitish false membrane, which soon disappears, exposing the dark-coloured spore-masses.

Spores yellowish-brown, globose to subglobose when seen flat; compressed laterally, and appearing oblong when seen edgewise; smooth, average 13–14 μ diam. or 13–17 × 8–14 μ, intermixed with hyaline, short, thread-like filaments derived from the stroma.

Sterile cells scattered among the spores, large, colourless, sometimes at least twice as large as the ordinary spores, and round or irregular in shape, owing to undergoing gelatinization

On *Fimbristylis* sp.

Queensland—Brisbane River (Bailey).
Victoria (Mrs. Martin).

Fimbristylis is a small grass-like sedge, and when growing on wet undrained land, the smut is very abundant in some seasons. This was made the type of a new genus founded by Cornu and differs from Ustilago in the formation of a stroma or compact mass of filaments, from the outside of which hyphae project, in which spores are successively developed.

Spore formation.—A section of the stalk shows the persistent mycelium in the diseased portions composed of delicate colourless hyphae which become aggregated into a dark-brown stroma around the medulla, and fibro-vascular bundles.

Arising from the stroma and directed outwardly are dark-brown strands of hyphae, slender and long-jointed, with the fertile hyphae between forming pockets or compartments of spores which are at first young and pale and gradually become dark and mature. The outer spores are at first held together by the remains of the strands from the stroma, but on maturing gradually separate.

(Plate XXXVII.)

Carex.

21. **Cintractia caricis** (Pers.) Magn.

Magnus, Abh. Bot. Ver. Prov. Brand., XXXVII., p. 78 (1896).

Ustilago caricis (Pers). Ung. Einfl. Bodens, p. 211 (1836).

Anthracoidea caricis (Pers.) Bref. Unters. Gesammt. Myk. XII., p. 144 (1895).

Sori in ovaries, at first hidden by the perigynium, then exposed, protected at first by a white membrane composed of semi-gelatinized cells, which soon disappear.

Spores firmly agglutinated, dark olivaceous, generally irregular, polygonal, sometimes subspherical or ellipsoid, finely punctulate 16–23 × 9–15 μ.

On *Carex breviculmis* R. Br.

Victoria—Mount Blackwood, Jan., 1903 (Robinson).

Tasmania—Hobart, Dec., 1907 (Rodway).

The smutted ovary is hard and black on the outside as if the spores originated there, but the spore-forming layer arises exclusively in the epidermis, the cells of which are ruptured by the expanding spores. They are at first minute, colourless, and of an irregular shape, and punctulate all over, then they become dark and opaque at the circumference, forming a dense mass of agglutinated spores. The fungus winters in the rhizome, so that the mycelium is perennial. Brefeld[5] has made this the type of a new genus, *Anthracoidea*, on account of the special mode of germination.

Germination.—The spores do not germinate at once but remain dormant till the following spring. Then they germinate in water and push forth a germ-tube into the air, which has not only a few septa, but is divided at the apex, so that each of the two cells produces ellipsoid conidia. The uppermost cell is elongated to form a sterigma—bearing conidia, which arise near one another and form an irregular head, if not interfered with. The ripe and fallen conidia do not sprout but only form simple germ-tubes, until their contents are exhausted.

It is this division of the apex of the aerial promycelium into two cells, each of which produces conidia, that Brefeld considered sufficiently distinct to form a new genus, which he named *Anthracoidea*.

(Plate XXXIV.)

Andropogon.

22. **Cintractia columellifera** (Tul.) McAlp.

Ustilago carbo, var. *columellifera* Tul., Ann. Sci. Nat. Bot. p. 81 (1847).

Sori in ovaries which are at first enclosed in the glumes. The walls of the ovary are brown and firm, forming a continuous membrane, but gradually decay in patches, exposing the dense agglutinated mass of dark-brown spores with a central columella of plant tissue.

Spores pale-brownish to olive-brown, smooth, globose to subglobose, with finely granular vacuolated contents, very regular in size, 7 μ diam., occasionally 8 μ.

On *Andropogon australis* Spring.

Queensland—Rockhampton (National Herbarium).

This species is labelled *Ustilago carbo* var. *columellifera*, but the development of the spores from the central columella outwards indicates that it belongs to the genus *Cintractia*.

Spore formation.—A cross-section made just at the base of the ovary where it joins the stalk shows a central core of plant tissue, consisting of fibro-vascular and parenchymatous tissue. Fungus filaments permeate it towards the outside and appear as a layer from which the spores are produced. At the base the younger spores are seen which pass into the mature form and constitute a dense dark agglutinated layer, the whole being at first enclosed in the wall of the ovary.

I am indebted for the determination of this host-plant to Professor Ewart, Government Botanist, but when distorted by the fungus, determination is rendered difficult.

It differs from *U. Ischaemi* Fckl., found on the same genus, in which the sori often involve the entire inflorescence, reaching a length of 10–30 mm., and provided with a fungus membrane which soon ruptures.

(Plate LIII.)

Panicum.

23. **Cintractia crus-galli** (Tr. and Earle) Magn.

Magnus, Ber. Deut. Bot. Ges. XIV., p. 392 (1896).
Sacc. Syll. XIV., p. 421 (1899).

Ustilago crus-galli Tracy and Earle, Bull. Torr. Bot. Club, XXII., p. 175 (1895).

Cintractia seymouriana Magnus, Ber. Deut. Bot. Ges. XIV., p. 217 (1896).

Forming large irregular or elongated swellings which are thrown into numerous brain-like folds, generally largest and most condensed at the nodes and elongated or less swollen along the internodes, up to 9 cm. long and 3 cm. at broadest part; isolated minute pustules also occur only 2 mm. long, involving the panicles, but very rarely on leaves.

The sori are protected by a tough hispid membrane, which is derived from the parent plant as it contains fibro-vascular bundles, and this membrane ultimately ruptures irregularly, disclosing the black powdery spores.

Spores formed from a matrix or stroma and arranged in rows with separating walls between of long-membered hyphae, globose to ellipsoid, olive-brown, densely echinulate, 8–11 μ diam. or 8–10 × 6·5–7 μ, occasionally reaching a length of 11·5 μ.

On *Panicum crus-galli* L.—Barnyard-grass.

New South Wales—Rooty Hill, March, 1906 and March, 1907 (Hattrick).

The plants were found growing in sandy soil and quite a number of them were affected. In some cases, a healthy inflorescence was produced from a lower node, and a large gall formed around an upper node, while the inflorescence proceeding from it would be destroyed by the smut. In other cases, several larger or smaller galls would be formed at a lower node and

the panicle proceeding from it would be affected by the smut, but from higher nodes of the main stem a healthy panicle would be produced. Galls were also formed on the stem independent of the nodes. The membrane consists of epidermis slightly cuticularized with elongated hairs, large-celled cortical parenchyma with starch granules and fibro-vascular bundles showing spiral vessels.

This species is widely distributed in North America and in the numerous American specimens examined by Magnus, the swellings or galls occurred on the upper internodes of the stem, seldom on the long internodes beneath the well-developed inflorescence, and very rarely on the leaves. The host-plant is cosmopolitan and considered by the late Baron von Mueller to be indigenous to Australia.

Spore formation.—In small and presumably young galls the individual spores were seen at different stages of development, imbedded in a gelatinous mass, due to deliquescence of the hyphae and small portions of the delicate and distinct hyphae were still visible. Magnus[3] has clearly described and illustrated the formation of the spores. Plate-like outgrowths from the axis penetrate the pustule and branch in various directions (Pl. XXXV., Fig. 79). Among these cells as well as those of the axis itself, a mycelium grows and spreads and forms a fungus layer both at the base of the pustule and on the surface of the plate-like outgrowths. This constitutes the matrix or stroma formed by the intercellular mycelial filaments interwoven with one another into a felt-like mass. It is from this matrix the upright hyphae proceed, in which the spores are formed (Pl. XXXV., Fig. 80). The spores are first formed at the base of the filaments and proceed outwardly in rows, while separating them into compartments are strands of the elongated hyphae. Not infrequently such a compartment may be further subdivided by the development of a new strand of hyphae, showing that the matrix still retains the power of forming either sterile or spore-forming hyphae.

It is worthy of notice that the formation of new spores at the base begins with a characteristic twisting of the hyphae into a ball. As the hyphae unroll and become upright, the spores begin to appear.

Germination has not been described.

(Plates XXI., XXXV.)

Rottboellia.

24. **Cintractia densa** McAlp.

Sori produced in inflorescence, destroying the individual florets, and arranged in compact dark-brown masses along the rachis, at first covered with greyish membrane, but soon falling away and exposing the spores.

Spores brownish, globose to subglobose or ellipsoid, with finely granular contents, smooth, 6·5–9·5 μ diam. or 9–9·5 × 6·5–8 μ.

On *Rottboellia compressa* L.

Victoria—Burnley, near Melbourne, Nov., 1892 (Robinson). Whittlesea Ranges, Nov., 1898 (C. French, jun.). Killara, Oct., 1902, March, 1903, Oct., 1906, March, 1907 (Robinson). Ararat, May, 1904 (C. French, jun.). Killara, March, 1908. River Flats, Shepparton, April, 1909. Near Melbourne, Dec., 1909 (C. French, jun.).

The spores form dense compact masses along the rachis which is sometimes $5\frac{1}{2}$ cm. long.

Spore formation.—A cross-section of the rachis shows the plant tissue in the centre and outside of the fibro-vascular bundles is the compact mass of filaments from which the spore-bearing hyphae are produced. These projecting hyphae produce the minute colourless spores at once, which gradually become brown and mature towards the outside. The young spores at first are rather angular, but as they approach maturity they become ellipsoid. Interspersed here and there among the fully formed spores are groups of cells with colourless and gelatinized walls, identical with those of the outer membrane.

Germination.—The smutted grass was very common at Killara in Oct., 1906, and the spores germinated freely in water, both at that time and several months later. The promycelium was four-celled, with a length of 36 μ and 3 μ broad, the protoplasm at first being highly vacuolated before the septa were formed. Conidia are produced both laterally and terminally, and sometimes as many as three are formed at the apex in a tri-partite manner. They are cylindrical to fusiform, 6–7 μ long, and produce secondary conidia while still attached. Spores were taken from specimens obtained in March, 1903, and they also germinated freely, showing that they are able to retain their germinating power for nearly five years.

(Plates XXIII., XXXVI., LIII.)

Distichlis.

25. **Cintractia distichlydis** McAlp.

Sori surrounding internodes usually for their whole length, at first enveloped by the leaf-sheaths and also covered by the epidermis, which gradually breaks away, exposing the dark-brown dense spore-masses.

Spores bright olivaceous individually, globose to shortly ellipsoid, smooth, minute, 5–6 μ diam. or 6–7 × 4–5·5 μ.

On *Distichlis maritima* Rafin.

Victoria—Oct., 1891 (National Herbarium—C. French, jun.). Elsternwick, March, 1900 (C. French, jun.). Sandringham, Sept., 1905. Elsternwick, Feb., 1910 (Brittlebank).

This grass is sometimes much reduced in size owing to the fungus.

Spore formation.—Sections of the diseased stems show the tissues of the plant in the centre and on the outside of the fibro-vascular bundles the spore-forming hyphae arise. The hyphae with elongated joints soon begin to form spores which are at first minute, rounded and colourless, but gradually towards the circumference they increase in size, assume an olivaceous tint and become mature.

Ustilago hypodytes (Schl.) Fr., is given on this host in Arizona by Clinton[4] and while there is a general resemblance, yet on comparing the spores of *C. distichlydis* with those of *C. hypodytes* the average size of the former is seen to be decidedly larger than the latter.

Germination.—This takes place equally well in water or in a nutritive solution such as somatose, in the course of 24 hours. The germ-tube is elongated, 1–4 septate, with finely vacuolated contents at first, then granular, 30–54 μ long and 3 μ broad. Conidia are produced both laterally and terminally, generally on slender stalks. They are oval, hyaline, with finely granular contents, 4–7 μ long, and sometimes two may be produced at the apex.

(Plates XXIV., XXXVI.)

26. **Cintractia exserta** McAlp.

Sori in spikelets, at first enveloped by a grayish membrane which gradually decays, exposing the dark-brown to black mass of spores. The elongated spore-mass, generally about ¾ cm. long, consists of several diseased and deformed spikelets blended together and a central core of plant tissue running through.

Spores olivaceous, smooth, globose to subglobose, or shortly elliptical, sometimes slightly angular, 6–8 μ diam. or 6–8 × 6–6·5 μ.

On *Anthistiria ciliata* L. f.—Kangaroo grass.

Victoria—Kiewa Valley, Nov., 1902 (Robinson). Plenty Ranges, Nov., 1909 (C. French, jun.).

In order to understand the appearance presented by this smut, it is necessary to know the structure of the normal inflorescence. The fertile spikelets bear a long, rigid, sinuous awn, over 6½ cm. long, and this has generally disappeared in diseased specimens so that they are readily recognised. The ovaries are also shortly stalked, and since the development of the ovary is prevented by the smut, it is the stalk which is distorted and destroyed by it. Several undeveloped spikelets have become blended together, so that in longitudinal section there are several such stalks seen.

Spore formation.—In a cross-section of a diseased spikelet the relation of the various parts is clearly seen. There is an outer colourless layer of tissue, representing the enveloping membrane and consisting of an epidermis of flattened cells and fungus filaments beneath. There is also a central core of plant tissue, consisting of parenchymatous cells studded with fibro-vascular bundles, and the whole is surrounded by a ring of fibro-vascular bundles. The parenchymatous tissue and a portion of each bundle are stained blue by Schulze's solution, showing the presence of starch. Between the central core and the outer membrane there is a dense mass of spores, the formation of which is clearly seen. Surrounding the ring of fibro-vascular bundles is the colourless stroma from which proceed the spore-bearing filaments. The spores are seen at first as minute colourless points, soon assuming a round or oval shape. They are at first embedded in the gelatinous mass formed by the deliquesced walls of the spore-bearing hyphae. Gradually they become more or less rounded in shape, acquire an olivaceous tint, and with a firm wall they become the mature spores. They are closely aggregated together towards the outside and the development is clearly from the centre outwards, all the hyphae being spore-forming.

Scattered among the spores here and there and sometimes forming chains as in Plate XXXVIII., Fig. 100, there are colourless cells, generally resembling those inside the epidermis forming the membrane, but they are as a rule larger, thicker walled, and apparently undergoing rapid division. They are stained yellow by Schulze's solution like the cells of the membrane. The origin of these cells is apparent, and may be traced to the inner layer of the membrane. The sterile fungus threads constituting the membrane tend to break up towards the interior into their component cells or rows of cells. The individual cells become globose or oblong with much-thickened walls, which always remain hyaline, and these cells become detached and mixed up with the spores.

(Plates XVI., XXXVIII.)

27. **Cintractia hypodytes** (Schl.) Dietel.

Dietel, Hemibasidii in Engl. and Prant. Naturl. Pflanzenf., p. 8 (1900).

Sori linear, at first covered by sheath, extending the entire length of the upper internodes and completely surrounding them with a firm blackish coat of agglutinated spores, which ultimately become powdery.

Spores in a dense layer, minute, dark olivaceous, globose or shortly ellipsoid, with granular contents, smooth, held together by a gelatinous material, 4–5 μ diam. or 4–6 × 3–4 μ.

On *Dichelachne crinita* Hook f.

Victoria—Ardmona, 1895 (Robinson). Emerald, March, 1907 (McLennan). Dookie, Dec., 1907. Dookie, Nov., 1908 (Brittlebank). Myrniong, Jan., 1910 (Brittlebank).

South Australia—Banks of Torrens River, Adelaide, Oct. (Tepper).

On *Stipa flavescens* Labill.

Victoria—Myrniong, Nov., 1904.

On *Stipa setacea* R. Br.

Victoria—Ardmona, Nov., 1898 and 1899 (Robinson); Myrniong, Dec., 1897 and 1902 (Brittlebank).

The upper internodes particularly are more or less completely surrounded throughout their entire length and the pedicels of the spikelets are often affected.

Generally the sheath encloses the diseased portion and there is little or nothing to indicate a smut beyond the absence of an inflorescence.

Spore formation.—A cross-section of the stem shows the tissues of the plant to be apparently unaltered, only the surface composed of the epidermis is rather irregular in its outline. The mycelial hyphae ramify in the parenchymatous cells and reaching the surface form a compact gelatinous mass of filaments. The outwardly directed spore-forming hyphae show the spores in various stages of development, at first minute and colourless and radiating in lines until they become fully mature and coloured. They form a continuous dense layer on the outside, where they are held together by a gelatinous material, but when thoroughly mature they fall away readily from the dry stems.

A specimen of *Ustilago hypodytes* (Schl.) Fr. on *Stipa spartea* Trin., in Clinton's Exsicc. Ustilag. C. 71, showed the same structure and in sections where spore-formation was not too far advanced the spores were seen to be formed from the inside outwards.

Germination.—A brief description has been given by Brefeld[1] and an illustration by Winter[1]. Brefeld says that the spores germinate readily in water and in nutritive solutions they form mycelial hyphae, but in numerous cultures long-continued he did not succeed in obtaining conidia. Winter, however, figures a spore germinating with one conidium. Plowright[1] says—"Although I have tried many times, I have never succeeded in getting the spores of this species to germinate," and yet according to Berkeley[2], the smut may be preserved in a garden for years by simply introducing infested plants.

(Plate XXXIV.)

28. **Cintractia leucoderma** (Berk) P. Henn.

P. Hennings, Hedw. XXXIV., p. 335 (1895).
Sacc. Syll. XIV., p. 420 (1899).

Ustilago leucoderma Berk. Ann. Mag. Nat. Hist., 2 Ser. IX., p. 200 (1852).
Cintractia krugiana Magn. Engl. Jahrb. XVII., p. 490 (1893).

Sori surrounding flower stalks and stems, forming conspicuous elongated bodies 3–30 mm. long, covered with a thick white crust of false membrane, which gradually flakes away, leaving exposed the dense black spore-mass.

Sterile pale coloured thin-walled cells, scattered among the spores, with margin rather irregular, due to gelatinization.

Spores dark-brown, opaque, finely warted, globose to oblong or angular, 13–16 μ diam. occasionally 18 μ long.

On *Rynchospora aurea* Vahl.

Queensland—Bundaberg (Bailey).
Queensland—Gatton, Sept., 1898 (Shelton, per Bailey[9]).

The clear colourless spores produced inside gradually assume a smoky-brown colour, then become darker towards the outside, and gradually fall away as they mature. Although Berkeley describes the spore as smooth, it is decidedly but finely warted.

The thick white crust constituting the false membrane is very conspicuous and may gradually become detached and fall away piecemeal from the host-plant.

It is interesting to trace the history of this species from its earliest naming by Berkeley, in 1852, until it was changed to *Cintractia leucoderma* by P. Hennings in 1895. The original specimens were found on the sheaths of some Sedge in the island of Saint Domingo, investing them with a white rugged crust, and the spores were described by Berkeley as being perfectly smooth, and 17 μ in diam. Next it was recorded on *Cyperus rotundus* L. (Nut-grass) from Queensland by Dr. Cooke in 1892, and by F. M. Bailey in 1898. In 1893 Magnus determined a smut on *Rynchospora gigantea* Willd. as *Cintractia krugiana*, which P. Hennings showed in 1895 to be a synonym of this species and therefore named it *C. leucoderma*.

Finally in 1890, Saccardo determined a smut on Danthonia from Victoria as *U. leucoderma* Berk., but on receiving a specimen of the same material from Professor Ludwig, I found it to be the common species on this genus of grasses, viz., *U. readeri* Syd. A specimen from the National Herbarium labelled *Ustilago leucoderma* on Cyperus ? was forwarded to Miss Annie Lorrain Smith of the British Museum. She determined it as *Cintractia leucoderma* and was able to settle the identity of the host-plant as *Rynchospora aurea* Vahl. The National Herbarium specimen said to be on Cyperus is probably the same as the specimen from Bailey in which case the only host is Rynchospora.

Germination not described.

(Plate XXXVII.)

29. **Cintractia sorghi-vulgaris** (Tul.) Clint.

Clinton, Bull. Ill. Agr. Exp. Sta. No. 47 (1897).
Sacc. Syll. VII., p. 456 (1888).

Sporisorium sorghi Link (1825).
Tilletia sorghi-vulgaris Tul. (1847).
Ustilago sorghi (Link) Pass. (1873).
Ustilago tulasnei Kuehn (1874).
Sphacelotheca sorghi (Link) Clint. (1902).

Sori generally in the ovaries, occasionally in the stamens, forming oval to oblong or cylindrical projecting bodies up to 6 mm. in length, at first protected by a fungus membrane which ultimately ruptures at the top, allowing the escape of the dark-brown spore mass and exposing the distinct columella composed of plant tissues.

The fungus membrane is composed of hyaline, subglobose to oblong cells, on an average 9–13 μ long.

Spores more or less agglutinated, globose to subglobose or occasionally shortly elliptical, dark-brown in the mass but brownish-olive individually, smooth, average 6 μ diam. and varying from 5·5 to 7 μ.

On *Andropogon sorghum* Brot. occurring on the varieties broom corn, amber cane, and sugar sorghum.

Queensland—(Bailey).

Victoria—Ardmona, 1895 (Robinson). Tatura, Feb., 1903 (Baldwin). Tungamah, Feb., 1908 (Mallows); March, 1909. Lake Rowan, March, 1909. Macorna, June, 1909 (McDonald).

The grain is converted into an enlarged projecting body consisting of the firm fungus membrane on the outside and the slender columella is often seen remaining in the centre after the bulk of the spores have been scattered.

This smut has been placed under various genera, as seen from the synonyms, but the mode of spore-formation shows that it belongs to Cintractia. *Ustilago cruenta* Kuehn, is also found on Sorghum, but instead of being confined to the flower it may occur on any part of the panicle, and even on the stem, while the spores are also larger on the average.

Germination.—The spores germinate readily in water within 24 hours, forming a 3–4 celled promycelium. Conidia are produced terminally or laterally, but not usually in great abundance. Buckle or knee joints are commonly formed by the promycelium, and from these, as well as from the end of the promycelium, slender threads are produced, supposed to be infection-threads. In a nutritive solution, germination is more luxuriant, more conidia are formed, and either when connected or detached, they give rise to secondary conidia by sprouting in a yeast-like manner. Finally, when the nutrition becomes exhausted, these conidia throw out slender germ-tubes.

(Plates XIV., XXXIX.)

Spinifex.

30. **Cintractia spinificis** (Ludw.) McAlp.

Ludwig, Zeitschr. Pflanzenkr. III., p. 138 (1893).
Brefeld, Unters. Gesammt. Myk. XII., p. 106 (1895).
Sacc. Syll. XI., p. 231 (1895).
Ustilago spinificis Ludw.

Sori in spikelets generally concealed by the glumes, destroying ovaries and forming a dense tough brownish mass of spores.

Spores globose to shortly ellipsoid, pale olivaceous to brownish, very minute, epispore finely punctulate, 3–4 μ diam. or 5 × 3 μ.

On *Spinifex hirsutus* Labill.
South Australia—Near Port Adelaide, Dec., 1892 (Tepper).

In the large dense globular head of this grass all the ovaries were destroyed and more or less completely replaced by a mass of spores which remain firmly united. This grass is often called the "Spiny Rolling Grass," since the flower heads of the female plant become detached on ripening and are easily rolled about by the wind, at last sticking in the sand, and the individual spikelets separate. In this way the smut, like the plant itself, is widely distributed and probably occurs all round the Australian coast.

Brefeld[5] has specially examined this species and found that in water the spores readily separate.

Spore formation.—A cross-section of the ovary shows the plant tissue in the centre with the surrounding spores embedded in it. The plant tissue consists of the large-celled parenchyma studded with fibro-vascular bundles, in which numerous vessels are visible. Towards the outside there is a dense layer of exceedingly fine fungus filaments felted together, yellowish in the mass and forming a stroma from which numerous slender hyaline fungus filaments project. In these the spores are developed, at first as minute colourless points, which gradually increase in size and assume a dark tint towards the outside, until finally they form the dense firm brownish mass of mature spores, arranged in rows and embedded in a gelatinous material. They burst through and rupture the epidermis as they become mature, and the unbroken epidermis may be seen alongside.

The spores are also formed in the interior, in cavities in the tissue. Surrounding the cavity there is the dense yellowish stroma from which the sporogenous hyphae project towards the centre and ultimately the cavity is filled with a dense mass of spores which escape by disruption of the tissue.

Germination.—The spores germinated after being kept for about two months, *not in water in which they remained unchanged*, but directly on the addition of nutritive solution. The promycelium was typically four-celled and relatively large in comparison with the spore, each individual cell being about equal in length and thickness. Below each septum and at the apex, elongated conidia are slowly formed which multiply by a process of yeast-like budding. Just before the solution is exhausted, the conidia may grow out into filaments, and if these reach the air they form *aerial conidia*. So general and so copious is this development in contrast to the rather sparing multiplication within the solution, that the conidia form a fine film on the surface like delicate down.

(Plate XXXII.)

SOROSPORIUM Rud.

Sori in various parts of the host, forming dark-coloured dusty spore masses. Spore-balls composed of numerous spores, often rather loosely united and at maturity completely separating.

Spores usually of a deep-brown colour.

Germination similar to that of Ustilago.

The spore-balls are temporary, and when the spores entirely separate, as they often do, at maturity, the genus cannot be distinguished from Ustilago. In such a case it is necessary to examine young stages and see the young spore-balls. It is not surprising, therefore, that several Sorosporiums have been described as Ustilagos. On the other hand, this genus is sometimes mistaken for Thecaphora and Tolyposporium, in which the spore-balls are permanent. The sori are often provided with a false membrane, and the order of development of the spore-balls is centrifugal, the youngest being at the centre.

Australian species, 13.

Aristida.

31. **Sorosporium consanguineum** Ell. and Ev.

Ellis and Everhart, Journ. Myc. III., p. 56 (1887).
Sacc. Syll. VII., p. 514 (1888).

Ustilago aristidae Peck, Bull. Torr. Bot. Club, XII., p. 35 (1885).

Sori in ovaries and entirely enclosed by glumes, but sometimes the black mass shines through them.

Spore-balls irregular, subspherical to elongated oblong, up to 130 μ in length, at first firm but afterwards readily separating and in old specimens becoming completely broken up. Spores mostly polygonal, also subglobose to ovoid, smooth, or very finely echinulate, yellowish-brown, but dark-brown in the mass, 7–10 μ long, but may occasionally reach a length of 13 μ.

On *Aristida arenaria* Gaud.
New South Wales—Namoi River, 1887 (National Herbarium).

On *Aristida behriana* F. v. M.
Victoria—Dookie, June, 1903 (Pye).
New South Wales—Narromine (Turner).

On *Aristida leptopoda*, Benth.
New South Wales—Liverpool Plains (Turner).

On *Aristida ramosa* R. Br.
New South Wales—Narromine (Turner).

On *Aristida vagans* Cav.
New South Wales—Wingello, March, 1900 (Maiden).
Coolabah, Dec., 1908 (Maiden).

On *Aristida* sp.
Queensland—(Bailey).

In the specimens examined, every seed seemed to be affected. The spores are generally smooth, but sometimes the epispore is finely echinulate.

Clinton has examined the types of the species of Peck, and of Ellis and Everhart, and found them to be the same; hence, by the law of priority, the smut ought to be called *S. aristidae.* But the name of *S. aristidae* Neg. is given by Saccardo in the Host Index of the Sylloge Fungorum, and as I can find no description of it, one cannot be sure that this and Peck's species are the same, so for the present the name had better be left unaltered.

The species on this host is entered as *U. segetum* in Cooke's Handbook.

Germination.—The specimen used was fully three years old, and the spores germinated in water. In the course of five days the spores had freely germinated, producing an elongated straight promycelium, often with vacuolated protoplasm, generally 4-celled, and 30–40 μ long, sometimes up to 50 μ. Conidia were produced at the apex, and laterally, oval in shape and about 5 μ long.

Norton[2], has also described the germination of this species. He found that germination begins almost immediately in water, and that a promycelium of 30–40 μ long is produced. Then a conidium is formed at the apex, three to four septa appear in the promycelium, and each cell produces a lateral conidium at its upper end. The conidia soon fall away. In nutrient solutions there is a similar but more vigorous germination.

(Plate XLI.)

Panicum.

32. **Sorosporium cryptum** McAlp.

Ustilago crypta McAlpine, Proc. Linn. Soc., N.S.W., p. 42 (1897). Sacc. Syll. XIV., p. 413 (1899).

Sori in spikelets, enveloped by the glumes, and ovaries converted into a black spore mass, with a central core of plant tissue; provided with an outer membrane.

Spore-balls somewhat evanescent, variable in size and shape, dark-brown when mature, oblong to oval or elongated ellipsoid, 80–150 μ long. Spores olivaceous, globose to subglobose or ellipsoid; epispore firm, brown, very delicately echinulate, but in many cases apparently smooth, 8–9 μ diam. or 7–10 × 6–8 μ.

On *Panicum bicolor* R. Br.

New South Wales—1896 (Maiden). Braidwood District, Feb., 1909 (Boorman).

On *Panicum effusum* R. Br.

New South Wales—Glenariff, Darling River (Turner).
Queensland—(Bailey).

Spore formation.—The spore-balls originate from the central core of plant tissue, from which strands of hyphal tissue proceed in a radiating manner, and in the compartments between, the spore-balls are developed. At first they are colourless and surrounded by an investment of gelatinous sterile hyphae then they become pale olive, and finally dark-olivaceous to brownish at maturity. The spore-balls are arranged in concentric circles around the central core of plant tissue, the outermost being fully formed and mature. Surrounding the outermost layer is a membrane consisting of epidermis and cortex of the host, lined by a yellow layer of sterile hyphae, which ultimately ruptures to allow the escape of the spore-balls.

The sterile hyphae are hyaline, closely septate, and the cells are either cubical or rounded.

Germination.—Spores were taken from *Panicum bicolor* nine months after being collected, and floated on water in a covered petri-dish exposed to the sun. After 41 hours they were germinating luxuriantly. The spore puts forth a promycelium which at first may be comparatively short and without septa (13 μ long) and yet give rise to a terminal conidium nearly as long as itself (10 μ). But generally the promycelia are septate, producing lateral as well as terminal conidia. Occasionally two promycelia may be produced from the same spore on opposite sides and branching may occur at the very base of the promycelium. Buckle or knee-joints are also met with. The conidia are elongated ellipsoid and vary in size. The apical conidium may elongate considerably, up to a length of 30 μ, becoming spindle-shaped and tri-septate, and two may be produced one after the other.

The spore may also give rise to an elongated slender promycelium in which the protoplasm collects at the end, and the terminal segment may become detached and produce slender filaments at either end. The promycelia may thus either give rise to ordinary conidia or segments may be detached, and in this way the smut is distributed.

Massee has determined a new species, *Ustilago confusa* on *Panicum paradoxum* R. Br., from Victoria, in which the spores have a tinge of violet by transmitted light, but there is not the slightest trace of it here, and since I am informed that there is no available material at Kew, it cannot be decided whether it is a Sorosporium or not.

There is a general resemblance to *S. syntherismae* (Pk.) Farl., but I have examined the specimen in Sydow's Ust. Exs. No. 41 on *Panicum proliferum* Lam., from Ohio, and the spores are darker in colour and the echinulation is much more pronounced.

(Plates XL., LVI.)

Anthistiria.

33. **Sorosporium enteromorphum** McAlp.

Ustilago enteromorpha McAlpine, Agr. Gaz., N.S.W., VII., p. 154 (1896).

Sori in florets, enclosed in a somewhat intestine-shaped gray membrane, at length brownish and decaying to allow the escape of the spores; spore-mass with membrane elongated and puckered, and sometimes coiled upon itself, half-an-inch to fully an inch long.

Spore-balls irregular, oblong to subglobose or elongated, 20–40 μ diam. or 30–60 μ in length.

Spores globose to oval, olivaceous, loosely adherent, 5–8 μ diam. or 6–10 × 4–7 μ; epispore thin, brown, very finely echinulate.

On *Anthistiria ciliata* L. f.—Kangaroo Grass.

Victoria—Near Melbourne, Dec., 1892 (Robinson). Dandenong Ranges, Jan., 1910 (C. French, jun.).

(Plates XVI., XL.)

Eriachne.

34. **Sorosporium eriachnes** Thuem.

Thuemen Symb. Myc. Austral. II., p. 4, No. 97 (1878).
Cooke, Handb. Austr. Fung., p. 328 (1892).
Sacc. Syll. VII., p. 514 (1888).
Ustilago australis Cooke, Grev. VIII., p. 34 (1879).

Sori in ovaries filling the glumes with a powdery mass of black spores. Spore-balls small, irregular.

Spores very variable in shape, irregular, angular or quadrangular, subglobose, or elliptic, smooth, opaque brown, 10–14 × 8–11 μ.

There are numerous large lemon-coloured smooth cells scattered among the spore masses, globose to subglobose or ellipsoid, with distinct thick walls 4–6 μ broad, 20–29 μ diam. or 19–29 × 13–16 μ.

On *Eriachne* sp.

Queensland—(Mueller); Muckadilla, 1897 (Bailey[8]).
New South Wales—(Mueller).

This genus of grasses is not represented in Victoria or Tasmania, although Cooke gives this smut as occurring in Victoria. A specimen labelled *Ustilago australis* Cooke was kindly sent by the Director of the Royal Gardens, Kew, and the spores were found in clusters although they readily fall away. Mueller had evidently sent a specimen of this smut both to Thuemen and the Kew Herbarium, and Cooke named it as above in his "Undescribed Fungi in the Kew Herbarium," overlooking the fact that it had already been named and described the previous year by Thuemen.

(Plate XLI.)

Eriochloa.

35. **Sorosporium mixtum** (Mass.) McAlp.

Tilletia mixta Massee, Kew Bull., p. 145 (1899).
Sorosporium eriochloae Griffiths, Bull. Torr. Bot. Club, XXXI., p. 84 (1904).

Sori in ovaries, oblong, about 2 mm. in length, enveloped by the glumes and concealed by a conspicuous whitish membrane which ruptures in lobes at the apex and exposes the black rather agglutinated spore masses, with remains of the aborted pistil in the centre; membrane composed of closely compacted hyaline cells end to end, oblong to cubical, with granular contents.

Spore-balls somewhat irregular, subglobose to oval or oblong, readily separating into their component spores, 40–80 μ or more in length.

Spores dark-brown, variable in shape and size, subglobose to oval or oblong, sometimes polygonal from pressure, finely echinulate, 13–15 μ diam. or 14–20 × 11–15 μ, average 16 μ long.

On *Eriochloa punctata* Ham.

New South Wales—Liverpool Plains, 1906 (Turner).

Eriochloa annulata Kunth.

New South Wales—Murrumbidgee, 1886 (Bennett).

This smut was originally found in Arizona on *Eriochloa punctata*. The specimen collected by Bennett in 1886 was sent to Kew, and a portion of the original material labelled *Tilletia mixta* was kindly supplied to me by the director.

(Plate XLI.)

Chamaeraphis.

36. **Sorosporium panici-miliacei** (Pers.) Takahashi.

Takahashi, Tok. Bot. Mag. XVI., p. 247 (1902).

Ustilago panici-miliacei (Pers.) Wint. Die Pilze, p. 89 (1884).

Sori produced in the inflorescence, destroying the spikelets and causing the ovary to swell, leaving the filiform spreading branches bearing them curled up, occasionally only a portion of the inflorescence attacked; epidermis of the host envelops the sori, together with a dense layer of sterile hyphae.

Spore-balls irregular in shape and variable in size, round to oval or oblong or polygonal, dark-brown, 50–100 μ long.

Spores yellowish-brown, subglobose to angular or ellipsoid; epispore firm, very finely echinulate, 9–13 μ diam. or 9–14 × 8–11 μ.

On *Chamaeraphis spinescens* Poir. = *Panicum spinescens* R. Br.

Victoria—Murray River, Jan., 1888 (Walter).

New South Wales—Near Corowa, Jan., 1906 (Pescott).

This was determined by Cooke as *U. cesatii* Waldh., but the examination of a portion of the original material from the National Herbarium showed it to be a Sorosporium. This is the first record of the species for Australia, and it thoroughly agrees with the characters given for it on Panicum miliaceum by Takahashi[1].

Spore formation.—The smut pustule is enveloped by the epidermis of the host and a relatively thick layer of sterile hyphae in close contact with it. It is also traversed longitudinally by the fibro-vascular bundles together with strands of sterile hyphae generally resembling those of the coating.

The spore-balls are formed in concentric rings around each fibro-vascular bundle, the youngest being innermost and the outermost often blending with those of adjoining bundles. The young balls have an investment of sterile gelatinous hyphae, but at maturity this has disappeared, being used up in the growth of the balls.

According to Trzhebinski[1] the spores adhering to the seeds of this smut are successfully destroyed by soaking the latter in a solution containing ·5 per cent. of copper sulphate and ·25 per cent. of formalin.

(Plate XL.)

Paspalum.

37. **Sorosporium paspali** McAlp.

Sori in inflorescence, usually destroying the whole, and leaving the elongated remains of the inflorescence surrounded by a black mass of spores.

Spore-balls dark-brown, globose to oblong or irregular, 30–40 μ in diam. or 30–50 μ long, at first firm, but afterwards readily separating.

Spores brownish individually, oblong to polygonal or pear-shaped, with thick epispore, smooth, variable in size, 12–18 × 9–14 μ, average 13–16 × 10–13 μ.

On *Paspalum scrobiculatum* L.
Queensland—(Bailey).

This specimen is given in Cooke's *Handbook of Australian Fungi* as *Ustilago cesatii* F. v. W., and as occurring in both Victoria and Queensland. Portion of the original material forwarded to Cooke shows it to be a Sorosporium, the spores being aggregated in balls and afterwards separating. The individual spores are smooth and not echinulate, so that it is quite a different smut.

(Plate XLIV.)

Scirpus, Juncus.

38. **Sorosporium piluliformis** (Berk.) McAlp.

Uredo piluliformis Berkeley, in Hook. Journ. Bot. II., p. 423 (1843).

Ustilago piluliformis (Berk.) Tulasne, Ann. Sci. Nat. p. 93 (1847)
Cooke, Handb. Austr. Fung., p. 325 (1892).

Ustilago marmorata Berkeley, Linn. Journ. XIII., p. 174 (1872).
Cooke, Handb. Austr. Fung., p. 325 (1892).

Ustilago muelleriana Thuemen, Myc. Univ. No. 623 (1879).
Cooke, Handb. Austr. Fung., p. 324 (1892).

Sori in ovaries, compact, sometimes causing a marbling of the unbroken epidermis which is ultimately ruptured and thrown off. Spore-balls generally in clusters of five or six, subglobose to oblong, dark olivaceous to dark-brown, readily breaking up after they are fully formed, 49–120 μ long.

Spores very irregular in shape and size, thick-walled, tuberculate, subglobose to oblong or polygonal, 10–18 μ long.

On *Scirpus prolifer* Rottb. = *Isolepis prolifera* R. Br.
South Australia—Mount Gambier, 1854 (Mueller, No. 94).

On *Juncus planifolius* R. Br.

Victoria—Near River Loddon (Mueller). Killara, March, 1907. Follett County, Dec., 1907 (Reader). Beech Forest, Dec., 1909. (Brittlebank).

New South Wales—Centennial Park, Sydney, Sept., 1900 (Cheel).

Tasmania—Hobart, Dec., 1891 and Jan., 1906 (Rodway).

The type material of *U. marmorata* has been examined from the National Herbarium. Berkeley in his original description, does not mention the portion of the plant on which the smut was found. Cooke in his *Australian Handbook* gives the leaves, while I have found it in the ovaries. I am indebted to the Director of the Royal Gardens, Kew, England, for a specimen of *U. muelleriana* Thuem.

Spore formation.—In a cross-section of the ovary the spore-balls are seen to be developed from the inside outwards, and if the spores were not in balls the species would be taken for a Cintractia. There is a central core of plant tissue consisting of parenchymatous cells together with smaller thick-walled cells. Surrounding this and radiating from it are very slender, delicate, wavy septate hyphae which proceed in strands to the circumference, and pockets are formed between the strands in which the spore-balls are formed. The spore-balls are at first minute and colourless, but gradually increase in size and become olivaceous until on arriving at maturity they are of a ruddy-brown colour. Intermixed with the mature spore-balls and also in the radiating hyphal strands, there are numerous colourless simple spore-like bodies which are ellipsoid, with coarsely granular contents, and generally averaging 9–10 × 5–6 μ. These spore-like bodies may be seen forming in chains in the hyphal filaments, and are probably abortive spores which have never advanced sufficiently to become spore-balls. Berkeley figures these abortive spores in his original article on *Uredo piluliformis*, and Tulasne in describing this form as *Ustilago piluliformis* refers to the spores being in clusters. This species is comparatively common on Juncus, but does not appear so frequently on Scirpus.

(Plate XLII.)

Zea.

39. **Sorosporium reilianum** (Kuehn) McAlp.

Kuehn, Rab. Fung. Eur. No. 1998 (1875).

Brefeld, Unters. Gesammt. Myk. V., p. 94 (1883).

Sacc. Syll. VII., p. 471 (1888).

Ustilago reiliana Kuehn.

Cintractia reiliana (Kuehn) Clint., Bull. Ill. Agr. Exp. Sta. No. 57, p. 346 (1900).

Sphacelotheca reiliana (Kuehn) Clint., Journ. Myc. VIII., p. 141 (1902).

Sori very prominent, blackish-brown, appearing in the tassels and ears and forming compact masses, which may include the entire inflorescence, at first enclosed in a pinkish to whitish membrane which soon ruptures, and the spores are dispersed, leaving the ray-like remains of the columella.

Membrane consisting of the outer tissues of the host-plant and sterile cells derived from the fungus, which form several layers of clear, more or less rounded cells, arranged in sub-spherical groups, and which may also occur mixed up with the spores.

Spore-balls dark-brown, globose to oval or irregular, firm at first, but afterwards readily separating, 80–112 μ in length.

Spores globose to subglobose, or sometimes slightly ellipsoid to ovoid, somewhat opaque, minutely but densely verruculose, 10–13 μ diam.

On *Zea Mays* L.—Maize.

Victoria—Orbost, April., 1901 (Pescott) and April, 1906. Lindenow, Feb.–May, 1908. Near Orbost, May, 1909.

New South Wales—Richmond, 1891. Singleton, May, 1899 (Waddell).

This species was at first recorded as *Ustilago maydis* Corda = *U. zeae* (Beckm.) Ung. by Dr. Cobb in New South Wales, but further investigation soon showed that it was not the ordinary Maize Smut of America. It is distinguished from that species by neither enlarging the ears nor forming large smut boils, by generally confining itself to the inflorescence and not attacking the leaves, and by the larger and more minutely verruculose spores. In addition, the spores are in balls at first and not solitary. It is fairly common in some of the later crops in maize-growing districts. In a specimen of *U. zeae* from Sydow's Ust. Exsicc. 157 on Maize from America, the spores were coarsely echinulate and 8–11 μ diam.

In the ovaries the membrane may envelop only spores mixed up with clusters of the sterile cells, or in other parts of the plant there may be a central core of plant tissues that have not been destroyed. The mycelium enters the grain from the base and gradually replaces the tissue of the ovary. At the base of the ovary you may still find some of the plant cells which have not yet been completely disintegrated, and at the top the membrane may be entirely composed of fungus cells. It is a case of gradual absorption of the plant tissues by the fungus. The systematic position of this smut has received considerable attention in America. Kuehn first named it *U. reiliana* in 1875, then Clinton called it *Cintractia reiliana*, and finally in 1902 *Sphacelotheca reiliana*. Norton[2] retained it as *U. reiliana*, although he observed that "the spores are aggregated in masses, and this species seems much like a *Sorosporium*, but until further studies of the development I have left it here." In a very young smut cob the spores are seen to be in clusters as shown in Plate XXX., so that its final resting-place is as a Sorosporium.

Germination.—This has already been described. The spore germinates readily in water in 21 hours, and forms both lateral and terminal conidia. In nutritive solutions there is a luxuriant development of conidia which sprout in a yeast-like manner and form colonies.

(Plates XII., XIII., XXX.)

Setaria.

40. **Sorosporium setariae** McAlp.

Sori destroying the entire inflorescence and converting the ovaries into a black powdery mass, or they may only affect one side of the inflorescence and sometimes the base, while the upper part is sound.

Spore-balls dark-brown, variously shaped, globose to oval, oblong to angular, consisting of numerous spores, varying in length from 60 to 160 μ.

Spores brown to olivaceous, globose, ellipsoid to angular, smooth, 10–12 μ diam. or 10–13 × 7–10 μ.

On *Setaria glauca* Beauv.

Queensland—Near Cloncurry, May, 1909 (Robinson).

This is the first Sorosporium found on this genus. A cross-section of the ovary shows that the spore-balls are developed around the vascular bundles, the youngest being nearest the bundle. Adjoining each bundle may be seen the gelatinized hyphae concentrically arranged and enclosing minute colourless points which afterwards become the spore-balls, and towards the circumference are the dark-brown spore-masses fully mature. There is also a central core of tissue around which the spore-balls are developed last of all, and the outer tissue of the ovary finally ruptures to allow of the escape of the powdery spore-masses.

Germination.—The spores do not germinate readily. After floating on water in a watch-glass for seven days, a few had put forth a colourless continuous germinal tube, usually without conidia, but, in some cases, with lateral and terminal conidia. The conidia were minute, about 3 μ long.

(Plate LIV.)

Schoenus.

41. **Sorosporium solidum** (Berk.) Mc Alp.

Ustilago solida Berk., Fl. Tasm. II., p. 270, (1860).

Urocystis solida Fischer von Waldheim, Aperçu syst. Ust, p. 38 (1877).

Sori in ovaries, black, compact, globose, shot-like.

Spore-balls subglobose to oblong or irregular, composed of 30 or more spores all similarly coloured when mature and somewhat firmly united, 50–70 μ long.

Spores dark-brown, smooth, with firm epispore, spherical to sub-spherical, elliptical or polygonal, 20–24 μ long.

On *Schoenus imberbis* R. Br.

Victoria—Cheltenham (Mrs. Martin). Nov., 1906 (Robinson).

Tasmania—Penquite, Dec., 1845 (Gunn.)

On *Schoenus apogon* Roem. and Schult.

Victoria—Dimboola, Nov., 1892 (Reader).

Tasmania—Hobart, Nov., 1894 (Rodway).

F. von Waldheim, who recorded this as a Urocystis, speaks of the glomerules of spores as having rarely three to four peripheral vesicles, but the examination of a large number of spores failed to reveal any distinct peripheral cells. But there are hyaline protuberances attached to the cells

which, probably, gave rise to this view. They are probably the remains of the enveloping hyphae, as they become detached and disappear on treatment with caustic potash. (Plate XLIII., Fig. 136).

Spore formation.—In a cross-section there is a central mass of parenchymatous plant cells, which are penetrated by colourless hyphae towards the outside. These give rise to a dense mass of olivaceous hyphae surrounding the central core of plant tissue, and one portion of the hyphae becomes spore-forming while the other remains sterile. The sterile portion forms strands of pale-coloured hyphae radiating towards the circumference, which are slender, elongated, and regularly and closely septate. Between the strands of sterile hyphae there are colourless hyphae, at first twisted into balls, and gradually these become definite, colourless spore-balls. They increase in size, the cell-wall becomes clearly defined, assumes a dark-brown colour, and the whole forms a fairly solid mass at the outside. The spores may partially separate from each other and are mixed up with shreds of the tissue of the ovary, and the broken-up remnants of the sterile hyphae.

The structure is clearly seen in Plate XLIII., Figs. 132, 133, where from the central core of plant tissue radiating strands of very fine septate filaments proceed and form, as it were, so many compartments in which the rows of spores are developed. The spores are seen in every stage of development, from the minute colourless spore, then with transverse and radiating septa, and finally as a dark-brown cluster of spores.

(Plates XXV., XLIII.)

Stipa.

42. **Sorosporium tumefaciens** McAlp.

Sori attacking and destroying entire inflorescence while still partially enclosed in sheathing blade. The entire panicle becomes swollen, dirty white to brownish, rupturing irregularly to allow the escape of the powdery spore-balls, up to 5 cm. in length.

Spore-balls globose and ellipsoid, oblong or irregular, olivaceous to dark-brown, 50–80 μ long.

Spores olivaceous to brownish, somewhat firmly united together, globose to ellipsoid or slightly irregular, smooth, often guttulate, especially when germinating, 8–10 μ diam. or 8–10 × 6.5 –7.5 μ., occasionally 11.5 μ long.

On *Stipa* sp. and *Stipa pubescens* R. Br.

Queensland—Near Cloncurry, May, 1909 (Robinson).

Sorosporium granulosum Ell. and Tracy, has been found on Stipa in America, but the spores are much larger, being 12–17 μ in length. A cross-section of an infected inflorescence, taken near its base, shows numerous vascular bundles completely surrounded by spore-balls, the younger and immature being towards the centre. The outer tissue is soon ruptured by the swelling spore-masses, which escape as a black powder, while the vascular bundles project in the form of numerous brown strands.

Germination.—This takes place readily in water, whether the spores are placed on a slide or floating on water in a watch-glass. In twenty-four hours numerous promycelia project from each spore-ball. They are hyaline, elongated, slender, septate, and bearing conidia laterally as well as terminally. The conidia are cylindrical, 6–10 μ long.

(Plate LIV.)

Eragrostis.

43. **Sorosporium turneri** McAlp.

Sori in ovaries, usually affecting each spikelet, ultimately exposed as a dense black mass, with the remains of the pistil usually projecting and a central columella of plant tissue.

Spore-balls irregular, subglobose to oblong, usually firmly united, 60–100 μ long.

Spores dark olive-brown, globose, with thin and smooth epispore, 10–11 μ diam.

On *Eragrostis nigra* Nees var. *trachycarpa*.

New South Wales—Near Armidale, New England (Turner).

The only two species of smut recorded on Eragrostis are *Ustilago spermophora* B. and C. in America and *Sphacelotheca strangulans* (Issat.) Clint. in Russia. The spores are echinulate or aculeolate in both.

(Plate XLIV.)

THECAPHORA Fingerhuth.

Sori in various parts of the host, but usually in the ovaries, forming a dusty spore mass at maturity.

Spore-balls light-coloured, composed of few or many spores, firmly and rather permanently united.

Spores smooth on contiguous sides but usually marked on free surface. Germination by means of an elongated septate mycelium, and as far as known, only producing a single conidium at the apex. This genus is distinguished from Sorosporium by the firmly united spores, and their being marked on the free surface but smooth on the united side.

Australian species, 2.

Lagenophora.

44. **Thecaphora lagenophorae** McAlp.

Ustilago lagenophorae McAlpine, Agr. Gaz. N.S.W., VI., p. 758, (1895).

Sori in ovaries, forming brown powdery spore-masses.

Spore-balls cinnamon-brown, sub-globose to oblong, composed of three to ten spores, firm.

Spores pale yellowish-brown, globose, sub-globose, or oval, warted on outer surface, but smooth where united, 18–22 μ diam.

On *Lagenophora emphysopus* Hook. f.

Tasmania—Mount Dromedary, at foot, Dec., 1894 (Rodway). Sandford, Jan., 1908 (Rodway).

The entire flower-head is converted into a mass of spores by means of this smut.

I did not succeed in getting the spores to germinate even when fresh, but the light-coloured spore-balls and the spores being smooth on the united face indicate this genus.

(Plate XLV.)

Leptocarpus.

45. **Thecaphora leptocarpi** Berk.

Berkeley, Linn. Journ. XIII., p. 388 (1872).
Cooke, Handb. Austr. Fung., p. 328 (1892).
Sacc. Syll. VII., p. 510 (1888).

Sori in ovaries, black, at first compact.

Spore-balls forming indefinite masses, varying in number of spores, but generally large.

Spores smooth, generally globose, sometimes shortly ellipsoid, yellowish-brown to dark-brown, 9–11 μ diam. or 9–12 × 7–8 μ

On *Leptocarpus tenax* R. Br.

Victoria—Wilson's Promontory, May, 1850 (National Herbarium).

Tasmania—Bellerive, near Hobart, May, 1889 (Rodway).

On *Leptocarpus* sp.

New South Wales—Upper Murray River, July, 1886 (National Herbarium).

The spores cohere well, but in the process of mounting for the microscope they break up into packets of various sizes.

(Plate LVI.)

TOLYPOSPORIUM Wor.

Sori in various parts of the host, but mostly in the ovaries, and forming a granular spore mass at maturity.

Spore-balls dark-coloured, composed of numerous spores permanently united.

Spores bound together by ridged folds or thickenings.

Germination similar to that of Ustilago.

The characteristics of this genus are the very firm spore-balls and the union of the individual spores by ridged folds or thickenings of their outer coats.

It is distinguished from Thecaphora by the dark-coloured spore-balls and the spores being inseparably united.

Australian species, 7.

Anthistiria.

46. **Tolyposporium bursum** (Berk.) McAlp.

Ustilago bursa Berkeley, Hook. Journ. p. 206 (1854).

Tolyposporium anthistiriae Cobb, Agr. Gaz. N. S. Wales, III., p. 1006 (1892).

Tolyposporium anthistiriae P. Henn. Hedw. XXXVII., p. 283 (1898).

Sori in spikes, and destroying them, cylindrical, 2–5 cm. long, at first covered by the yellow epidermis, then ruptured.

Spore-balls very black, rounded, oblong or polyhedral, variable in size, 40–150 μ diam.

Spores sub-globose or ellipsoid, cinnamon-brown, with thickish (1 μ) very finely punctulate epispore, 9–14 × 8–12 μ.

On *Anthistiria ciliata* L. f.—Kangaroo grass.

New South Wales—1892 (Cobb).

Victoria—Kiewa Valley, Nov., 1902 (Robinson).

Queensland—Walsh River (Bailey)[3].

Germination.—The spore germinates in water, giving rise to an elongated, septate promycelium, which bears lateral and terminal fusiform conidia, 5–10 μ long. The detached conidia bud in a yeast-like manner.

(Plate XVII., XLVI.)

Leersia.

47. **Tolyposporium globuligerum** (Berk. and Br.) Ricker.

Ricker, Journ. Myc. XI., p. 112 (1905).
Cooke, Handb. Austr. Fung. p. 328 (1892).
Sacc. Syll. VII., p. 509 (1888).

Thecaphora globuligera Berk. and Br. Trans. Linn. Soc., 2nd Ser., Vol. II., Pt. 1, p. 407 (1878)

Sori in ovaries, subglobose, 1–2 mm. diam., covered by yellowish-green smooth membrane, which ruptures and exposes the black masses of spores.

Spore-balls opaque, firm, composed of numerous spores, 50–200 μ diam. or even more.

Spores olivaceous to brownish, subglobose to angular, rough, and tubercular but not echinulate, generally polygonal, with obtuse angles by which they are united to each other, average 9–11 μ.

On *Leersia hexandra* Swartz—Rice grass.

Queensland—Brisbane River (Bailey).

This grass is common near water-courses and is often attacked by this smut.

The swollen ovary retains its outer coat while the contents are completely replaced by the spores.

The projecting processes of the spores and how they are united to each other is well shown in Plate XLV., and justifies the change in the genus made by Ricker.

(Plate XLV.)

Juncus.

48. **Tolyposporium juncophilum** McAlp.

Sori in the stems, forming dense powdery masses of spores which burst through and dust it over with a black powder.

Spore-balls opaque, composed of numerous, firmly united spores, subglobose to oblong or irregular.

Spores olive-brown, subglobose to ellipsoid or polygonal, epispore unequally thickened, smooth.

On *Juncus pallidus* R. Br.

Victoria—Cheltenham, Dec., 1909 (C. French, jun.).

New South Wales—Nov., 1901 (Helms).

Tasmania—Hobart, Jan., 1906 (Rodway).

West Australia—Mt. Barker, Oct., 1909 (Summers).

In *T. junci* (Schroet.) Woron. Schroeter says that the peripheral cells are shortly echinulate on the outer surface, but in this species they are perfectly smooth. In addition to this the spore-balls are generally more or less subglobose, while in *T. junci* they are elongated and contain fewer spores in the ball.

(Plate XLVII.)

Lepidobolus.

49. **Tolyposporium lepidoboli** McAlp.

McAlpine, Proc. Linn. Soc. N.S.W., XXIX., p. 127 (1904).
Sacc. Syll. XVII., p. 491 (1905).

Sori in ovaries, black, powdery, but completely enclosed in the small fruits, surrounded by the enveloping bracts.

Spore-balls composed of numerous spores, firmly united into irregular masses, subglobose to oblong, 80–120 μ long.

Spores olivaceous in mass, globose to subglobose, ellipsoid or polygonal, finely warted, 12–14 μ diam. or 12–16 × 10–11 μ.

On *Lepidobolus drapetocoleus* F. v. M.

Victoria—Dimboola, Jan., 1903 (Reader).

(Plate XLVI.)

Lepidosperma.

50. **Tolyposporium lepidospermae** McAlp.

Sori enclosed in spikelets and not visible to naked eye, except from the spore-balls, being scattered over the inflorescence, forming a black granular mass.

Spore-balls black, opaque, variable in size and shape, spherical to oblong, or irregular, 50–60 μ long, consisting of numerous spores firmly agglutinated together.

Spores brown to chestnut-brown, subglobose to ellipsoid or polygonal, strongly warted all over, variable in size, 15–17 μ long.

On *Lepidosperma angustatum* R. Br. = *L. viscidum* R. Br.
Victoria—Stawell, Feb., 1904 (Reader).

On comparing this species with that of *T. rodwayi* occurring on the same genus, it is found that the densely warted spores distinguish it at once. There are also fewer spores in the ball, as may readily be seen on comparing Plate XLVII., Figs. 154 and 155.

(Plate XLVII.)

Gahnia.

51. **Tolyposporium muellerianum** (Thuem.) McAlp.

Sorosporium muellerianum Thuemen, Symb. Myc. Austral. II., p. 5, No. 98 (1878).

Sori in spikelets, but scarcely visible to the naked eye.

Spore-balls black to dark-brown, sub-rotund to oblong or irregular, consisting of numerous firmly united spores, 40–50 μ diam., or 50–70 μ long, occasionally 80–90 μ.

Spores brown, pellucid, smooth, variable in shape, ellipsoid to polygonal or pear-shaped, and then sometimes slightly prolonged at the point.

On *Gahnia radula* Benth.
Tasmania—Hobart, Jan., 1906 (Rodway).

On *Gahnia trifida* Labill. = *Cladium filum* R. Br. (in part).
Victoria—Nhill, Nov., 1898 (Reader).

(Plate XLVII.)

Lepidosperma.

52. **Tolyposporium rodwayi** McAlp.

Sori enclosed in spikelets, not visible to naked eye, and forming a black granular spore-mass.

Spore-balls black, opaque, variable in size and shape, generally spherical to oblong or elongated oblong, 30–60 μ diam. or 50–100 μ long, consisting of numerous very firmly agglutinated spores.

Spores olivaceous to brown, smooth, ellipsoid to broadly oblong, occasionally with beak-like projecting, blunt processes on inner side, or wedge-shaped, and adhering together by dark folds of their membrane, 15–21 × 9–12 μ.

On *Lepidosperma laterale* R. Br.
Tasmania—Longley, Dec., 1891 (Rodway).

It is only by strong mechanical pressure that the spores can be separated and then only partially.

(Plate XLVII.)

TILLETIA Tul.

Sori in various parts of the host, usually in ovaries, generally pulverulent, black or blackish-olive, often foetid, especially when moistened.

Spores single, free, usually produced singly in the ends of fertile swollen hyphae, which generally disappear almost completely through gelatinization, of relatively large size.

Germination by means of a short promycelium which bears a terminal whorl of slender elongated conidia, and these often fuse in pairs, giving rise to slender secondary conidia on germination.

This genus differs mainly from Ustilago in the mode of germination of the spores, and where this is not known, species are placed here provisionally on account of the relatively larger size of the spores as compared with those of Ustilago.

Australian species, 6.

Festuca.

53. **Tilletia fusca** Ell. and Ev.

Ellis and Everhart, Journ. Myc. III., p. 55 (1887).
Sacc. Syll. VII., p. 484 (1888).

Sori in ovaries of each spikelet, oblong, 3 mm. long, showing as dark bodies while still enclosed by the glumes and afterwards rupturing to allow the escape of the spores.

Spores reddish-brown to dark reddish-brown, globose to ovoid or oblong, occasionally angular, with prominent regular reticulations; ridges showing at circumference as short blunt projections and enveloped by a clear membrane probably gelatinous; 23–25 μ diam. or 23–26 × 18–20 μ.

Sterile cells hyaline, relatively thin-walled, globose to oblong, generally smaller than the spores, 16–23 μ long.

Occasionally small brown cells occur, smooth and only about one-half the regular size, 10–13 μ.

Both the colourless and coloured cells with smooth walls appear to be immature spores, in the one case from not having attained the full size; in the other from not having developed the colouring matter.

On *Festuca bromoides* L.—Silver grass.
Victoria—Angustown, Dec., 1909, and March, 1910.

Although the Silver grass is widely distributed, I have not met with this smut but in the one locality, where it is fairly common. The species only occurs elsewhere in the United States of America, where it was first found on Festuca.

Germination.—Spores were placed on a slide in water which had been boiled, on 7th December, and it was only after 17 days, on 24th December, that germination occurred in a few. The promycelium was elongated, biseptate, with the vacuolated protoplasm transferred to the last segment. There were usually a crown of seven conidia at the apex, each elongated, slender, slightly curved and tapering, 66–72 μ long, and one pair were observed with a transverse bar uniting them near the apex.

(Plate LV.)

Hordeum.

54. Tilletia hordei Koern.

Koernicke Hedw. XVI., p. 30 (1877).
Sacc. Syll. VII., p. 484 (1888).

Sori in ovaries, which are at first dark-green in colour, ultimately black, concealed by the glumes, foetid, causing the spike to have a slight club-head appearance.

Spores black in the mass, brownish individually, globose to subglobose, occasionally ellipsoid, 19–20 μ diam. or 19–22 × 17–19 μ; epispore with raised ridges forming a network.

On *Hordeum murinum* L.—Barley grass.

South Australia—Orroroo District in the far north, Oct., 1909 (Summers).

New South Wales—Coolac near Gundagi, Nov., 1908 (Sullivan).

The odour is somewhat similar to that of Stinking Smut or Bunt of wheat, but the spores are larger and more regular in shape. The wall of the ovary still retains its texture and green colouring matter while enclosing the spores, but blackens as the spores mature.

The smut-ball is shorter and stouter than the healthy seed.

This species has only hitherto been recorded from Persia.

Germination.—This was tried in a variety of ways with fresh spores and spores a year old, but only in one instance did it occur with the fresh spores. Spores were floated on water, immersed in water, placed in hanging drop, on plaster of paris kept moist, and on damp blotting-paper. Nutritive solutions were also tried, such as sugar, ammonium nitrate, and infusion of wheat. The spores were carefully watched for about six weeks, but not the slightest attempt at germination was observed. However, on the 43rd day, the fresh spores, dusted on a slide and placed over a jar of water, were found to be germinating and producing the typical spores of Tilletia.

(Plate LVI.)

Deyeuxia.

55. Tilletia inolens McAlp.

McAlpine, Agr. Gaz. N.S.W., VII., p. 154 (1896).
Massee, Bull. Kew, p. 152 (1899).

Sori produced in inflorescence and on upper leaves, black, pulverulent, without smell.

Hyphae septate, hyaline 4–5 μ broad.

Spores regularly globose, dark-brown, 30–39 μ diam., average 34 μ; epispore covered with very coarse warts which project like so many blunt teeth, and the whole is enveloped by a fine hyaline membrane. The projecting teeth covered by the enveloping membrane, give the appearance of a pale yellowish or yellowish-brown border round the spore itself, 3–6 μ broad. Between the warts there are very minute projections on the epispore.

On *Deyeuxia forsteri* Kunth.

Victoria—Ardmona, Nov., 1894 (Robinson).

The large coarse projections on the surface of the spore are very pronounced, but the fine minute tubercles between are only to be seen by careful focussing and fine illumination, or when a spore happens to be crushed they may become plainly visible.

According to Massee this species appears to be closely allied to *T. rauwenhoffii F. v. W.* = *T. holci* (West.) Rostr., but an examination of the specimen in Sydow's Ustilagineen Exs. 372, shows the decided network of the epispore, which is quite distinct from the warts of *T. inolens.*

Germination not known.

(Plate XLIX.)

Triticum.

56. **Tilletia levis** Kuehn.

Kuehn, Hedw. XII., p. 152 (1873).
Massee, Bull. Kew., p. 144 (1899).
Sacc. Syll. VII., p. 485 (1888).

Ustilago foetens B. and C. in Grev. III., p. 59 (1874).
Tilletia foetens (B. and C.) Trelease, Parasitic Fungi of Wisconsin, p. 35 (1884).

Sori in ovaries, concealed by the glumes, dark-brown to olivaceous, foetid.

Spores black in the mass, pale brown to almost colourless individually, globose to elliptic, occasionally somewhat angular, very variable in shape and size, 16–18 μ diam. or 19–25 × 16–17 μ; epispore, smooth, $1\frac{1}{2}$–2 μ thick.

On *Triticum vulgare* Vill.—Wheat.

Probably in all the States of the Commonwealth, like *T. tritici.* This species generally resembles *T. tritici*, but the spore in addition to being smooth is more irregular in shape and size. Both species may occur in the same ear, but this is easily explained, as a number of spores may infest the one plant; and if the spores are mixed, then both forms might appear in the same ear. This smooth-spored form is not a mere variation of the species with netted epispore, for it has been used for infecting directly the different species and varieties of wheat, and it remained true to its characteristics. Both species were used for infecting wheat during the past season and invariably remained distinct.

The smooth-spored form appears to be more common than the other, at least in Victoria. This fungus was first named *Ustilago foetens* by Berkeley and Curtis in Ravenel's *Fungi Carol. Exsicc.* V., No. 100, 1860, but no description was published and so the name cannot be accepted. Then Kuehn in 1867 discovered the same form but only published his description in 1873, when he named it as above.

I have already referred to the amount of loss caused by this smut, and even in the present crop (October, 1909) the yield will be reduced by fully 5 bushels per acre in some parts of South Australia. It is also very noticeable that in consecutive plots grown under exactly similar conditions some varieties are much less susceptible than others. Thus Federation and Gluyas were badly affected, while Carmichael's Eclipse showed hardly a sign of it.

In some seasons, such as 1898, in which the summer is comparatively rainless, the smut-balls are harder and firmer than usual, so much so, that they give great trouble in the mill, since they do not break up as is usually the case. It is generally considered that the seed-case was dried up and had no opportunity of softening in the absence of rain. On examining sections of such hardened grains, it was found that the spores of the smut were not fully matured and that many of them were colourless. This would account for the spores forming a dense mass and sticking together, because it is only when they are fully mature that they fall away like powder. The drying up would also, of course, tend to make the entire grain firm and hard.

(Plates II., XLVIII.)

Lolium, Poa.

57. **Tilletia striaeformis** (Westd.) Oud.

Oudemans, Bot. Zeit. XXXVI., p. 440 (1878).
Sacc. Syll. VII., p. 484 (1888).

Tilletia de Baryana Fischer von Waldheim, Bull. Soc. Imp. Nat. Moscow XL., p. 251 (1867).
Ustilago striaeformis (Westd.) Niessl, Hedw. XV., p. 1 (1876).
Ustilago poarum McAlp. Roy. Soc. Victoria, VII. (New Series), p. 220 (1894).

Sori blackish to brownish-black, forming elongated streaks on the leaves, leaf-sheaths and occasionally found in the ovaries, at first covered, then free, becoming pulverulent.

Spores globose to ellipsoid or even somewhat angular, olive-brown prominently echinulate 10–13 μ diam. or 13–16 × 8–10 μ.

On *Lolium perenne* L.—Rye-grass.

Victoria—Creswick, Jan., 1892 (Robinson). Near Melbourne, Jan., 1901. Pakenham, Dec., 1900 (Robinson). Port Fairy, March, 1899 and Aug., 1900.

On *Poa annua* L.—Annual Meadow-grass.

Victoria—Ardmona, Oct., 1893 (Robinson).

This species occurs on quite a number of grasses, but it has only hitherto been found here on Rye-grass and Annual Meadow-grass. Every leaf of a plant may be affected and growth is naturally prevented. It is only rarely that in such diseased plants the ovaries are produced, and then they are completely destroyed by the smut.

This species was named *T. de Baryana* by Fischer von Waldheim[3], but he afterwards found, on examining the herbarium of M. Westendorp that the *Uredo striaeformis* of that author was the same species, and accordingly that specific name has been adopted. Niessl, however, considered it to be an Ustilago, and Clinton[4] still places this species under that genus, seeing that the germination of the spores has not been observed and that their general aspect is that of Ustilago. But as F. von Waldheim[2] has shown, the spores are formed at the end of spore-bearing filaments as in Tilletia, although the spore is surrounded by a gelatinous envelope up to the time of ripening. In the perfectly mature spore, however, there is no trace of it, and until its position is definitely settled by the germination of the spore it will be retained here.

(Plate L.)

Triticum.

58. **Tilletia tritici** (Bjerk.) Wint.

Winter, Die Pilze, p. 110 (1884).
Brefeld, Unters. Gesammt. Myk. V., p. 146 (1883).
Sacc. Syll. VII., p. 481 (1888).

Lycoperdon tritici Bjerk. in Act. Suec., p. 326 (1775).
Tilletia caries Tul. Mem. Ust., p. 113 (1847).

Sori in ovaries, blackish to olivaceous, more or less concealed by the glumes and all or only portion of the ovaries of a spike infected, foetid.

Spores spherical or sub-spherical generally, black in the mass, brownish individually, 15–20 μ, average 16 μ diam., but some may reach a length of 22 μ; epispore furnished with ridges 1–1·5 μ high and forming a network with meshes variable in size and shape, but generally 3–4 μ wide.

On *Triticum vulgare* Vill.—Wheat.

In all the States of the Commonwealth.

The spores are generally globose, but they are occasionally oblong to pear-shaped, and then they may reach a length of 22 μ. They emit an offensive odour something like stinking fish, and when the smut-balls are crushed or moistened it is more pronounced.

The name of *T. tritici*, although later in point of time than *T. caries*, is preferred, because, under the latter name, other species were included.

Germination.—This has already been fully described at p. 70.

(Plates II., XLVIII.)

ENTYLOMA De By.

Sori generally in the leaves and permanently imbedded in the tissues, usually forming discoloured but otherwise slightly altered areas.

Spores single, scattered in patches through the tissue and produced terminally or at intervals in the fertile hyphae, which do not disappear entirely through the gelatinization.

Germination similar to that of Tilletia and often in addition to the promycelial conidia, tufts of conidia are formed on protruding hyphae, which arise from the spore-bearing mycelium.

There is nothing characteristic about the spores to distinguish this genus, only they are free in the tissues, which are usually pale-coloured, with protruding conidial tufts.

Australian species, 2.

Eugenia.

59. **Entyloma eugeniarum** Cke. and Mass.

Cooke and Massee, Grev. XIX., p. 92 (1891).
Cooke, Handb. Austr. Fung., p. 327 (1892).
Sacc. Syll. XI., p. 233 (1895).

Sori in irregular dark-brown pustules, which are flattened, rounded, or confluent, and then angular, up to $\frac{1}{2}$ mm., collected in large patches on under surface of leaf.

Spores globose, oblong, or angular, with thick, smooth, pale-brown epispore, 10–20 × 10–12 μ, average 16 × 11 μ.

On leaves of *Eugenia*.

Queensland—Harvey's Creek (Bailey[4]).

Sections of the affected leaves show that they are sometimes confluent, and that they may extend almost from the bottom to the top of leaf.

(Plate L.)

Melilotus.

60. **Entyloma meliloti** McAlp.

Sori in leaves, forming on both surfaces minute, round, slightly raised pustules, generally brown at margin, and pale or dark-coloured at centre, often confluent and producing larger patches.

Spores colourless to honey-yellow, globose to ellipsoid or sometimes angular by pressure, smooth, 10–12 μ diam., or 11–13 × 9–9.5 μ.

On leaves of *Melilotus indica* All. = *M. parviflora* Des.

Victoria—Werribee, Oct., 1909 (C. French, jun.).

This is the first recorded species on Melilotus and even on a Leguminous plant, for *E. nectrioides* Speg. is doubtfully referred to this family. In sections of diseased portions of the leaf the spores are seen in great masses, and there are numerous fungus filaments ramifying among them.

(Plate LVI.)

UROCYSTIS Rab.

Sori usually in leaves or stems, and forming dark-coloured dusty spore masses.

Spore-balls permanent, with a special envelope of tinted sterile cells enclosing one or several fertile cells.

Spores usually dark-coloured and variable in size.

Germination by means of a promycelium, either undivided or divided into several cells, and bearing at its apex one or a whorl of elongated conidia, which give rise to similar secondary conidia or to infection threads.

This genus is often rendered conspicuous by the distortion produced in the affected parts. The cortex of sterile cells usually completely envelopes the fertile cells, but it sometimes only forms a partial envelope.

Australian species, 7.

Agropyron.

61. **Urocystis agropyri** (Preuss) Schroet.

Schroeter, Abh. Schles., Ges., p. 7 (1870).
Sacc. Syll. VII., p. 516 (1888).

Sori forming long parallel black lines on leaves and stems, at first covered by the leaden-coloured epidermis, then erumpent and pulverulent.

Spore-balls subglobose to oblong or ellipsoid, 20–30 μ long, but sometimes reaching a length of 42 μ.

Spores deep reddish-brown, subglobose to oblong or angular, 1–3 not uncommon in a ball, sometimes 4 and 5, varying in size, from 9–15 μ in length; sterile cells usually completely surrounding fertile cells, yellowish and elongated.

On *Agropyron scabrum* Beauv.

Victoria—River flats near Shepparton, Oct., 1896 (Robinson).

Kergunyah Hills, Nov., 1902 (Robinson).

This species is closely allied to *U. occulta*, and by some has been considered identical, but no cross-infections on wheat or rye have been undertaken with success. There is not usually the same rotundity about the spore as in *U. occulta*, but it is more angular, while the cell walls are thicker and darker.

Germination not known.

(Plate LII.)

Ranunculus.

62. **Urocystis anemones** (Pers.) Wint.

Winter, Die Pilze, p. 123 (1881).
Brefeld, Unters. Gesammt. Myk. XII., p. 176 (1895).
McAlpine, Agr. Gaz., N.S.W., VII., p. 155 (1896).
Sacc. Syll. VII., p. 518 (1888).

Sori on leaves, leaf-stalks, and stems, at first covered by the epidermis, then splitting longitudinally and becoming powdery, black; producing large irregular, gouty swellings.

Spore-balls very variable in size and shape, 15–33 μ long.

Spores 1–2 usually in a ball, occasionally 4–5, dark-brown, subspherical, to polygonal, obscurely punctate, 12–15 μ; sterile cells globose to somewhat oval, pale-brown or yellowish tinted, seldom completely surrounding the spores, not numerous, sometimes reduced to one or even wanting, 8–10 μ long.

On *Ranunculus* sp.

Victoria—River flats near Shepparton, Nov., 1895 (Robinson).

On the stems and leaf-stalks particularly, the tissue is abnormally thickened and broadened, giving rise to blister-like swellings.

This species is characterized by the small number of spores in a ball, and the sterile cells being reduced in number.

Germination.—This has been recorded and illustrated by Fischer von Waldheim[3], Plowright[1], and Brefeld[5]. Brefeld found that the spores did not germinate immediately, but only after half-a-year's rest in damp earth. When germinated in water they form a very short promycelium, and produce a whorl of conidia at the end. Plowright succeeded in infecting the foliage of *Ranunculus* with conidia, and remarks that—"This is one of the few species in which mycelium is localized, and the infection of the host-plant occurs at the same place at which the spores are subsequently formed."

(Plate LII.)

Wurmbea.

63. **Urocystis destruens** McAlp.

Sori in leaves, forming large swollen lines, at first covered by the greyish or leaden-coloured epidermis, then rupturing and exposing the black, pulverulent spore-masses.

Spore-balls generally globose or subglobose, 18–22 μ diam., or occasionally oblong, and reaching a length of 30 μ.

Spores yellowish-brown to dark-brown, firm walled, smooth, usually one, occasionally two, in ball, globose to subglobose or oval, 10–14 μ diam.; sterile cells pale-yellowish, globose to ellipsoid, completely surrounding spore or spores, 6–8 μ diam., or up to 15 μ long.

On *Wurmbea dioica* F. v. M.

Victoria—Near Melbourne, Sept., 1902.

This plant was in flower when this smut was obtained, and it affected the lower leaves badly, while the upper leaves merely showed indications of it.

There is generally only a solitary spore, and very occasionally two, but no more were observed.

Although this species was first referred to *U. colchici* (Schl.) Rab. in Proc. Linn. Soc. N.S.W., XXVIII., p. 102 (1903), yet on closer examination and comparison it is found to differ sufficiently to constitute a new species.

The specimen of *Urocystis colchici* from Sydow's Ust. Exs. No. 246 shows that while the spore-ball may consist of a single spore, there are frequently two and three or even four spores. The spores are of a sepia-brown, subglobose to ovoid or irregular oblong, 12–15 μ diam., or varying in length from 16–21 μ. The spore-balls may occasionally reach a length of 50 μ.

(Plate LII.)

Hypoxis.

64. **Urocystis hypoxydis** Thaxt.

Thaxter, Ann. Rep. Conn. Agr. Exp. Sta., p. 153 (1889).
Sacc. Syll. IX., p. 290 (1891).

Sori in the flowers, destroying and distorting them, also in the leaves, especially in the basal portion, causing irregular swellings, at first covered by the leaden-coloured epidermis, then rupturing to allow the escape of the black dusty spore-masses.

Spore-balls spherical to ovoid or oblong, 25–54 μ long.

Spores ruddy-brown, spherical to oval or polygonal, smooth, 1–8 but mostly 3–5 in a ball, 9–16 μ, average 13 μ long; sterile cells yellowish to pale transparent brown, oval to ellipsoid, completely covering the spores, about same length as spores but not so broad.

On flowers, leaves, and sheath of bulb of *Hypoxis glabella* R. Br.

Victoria—Ardmona, Oct., 1897 (Robinson). Warracknabeal, July, 1903, March, 1904 (Reader).

This species was found by Thaxter on *Hypoxis erecta L.* in Connecticut, but only on the flowers, pedicels, and peduncles.

Germination not known.

(Plate LII.)

Secale, Lolium, Poa.

65. **Urocystis occulta** (Wallr.) Rab.

Rabenhorst in Herb. Viv. Myc. II., No. 393 (1856).
Brefeld, Unters. Gesammt. Myk. XII., p. 175 (1895).
Sacc. Syll. VII., p. 515 (1888).

Sori in leaves, leaf-sheaths, stems, and glumes, forming long streaks, at first covered by the leaden-coloured epidermis, then erumpent, exposing the powdery and black spores.

Spore-balls globose, elliptical, or oblong, 20–36 × 14–32 μ, exceptionally 42 × 36 μ.

Spores dark golden-brown, spherical to oblong, 1–3 or occasionally 4–5 in a ball, 12–18 μ long; sterile peripheral cells generally partially, but sometimes completely, investing the spores, pale-yellowish, oval, 6–10 μ long.

On *Secale cereale* L.—Rye.

Victoria—On plants infected with spores from Germany.

On *Lolium perenne* L.—Rye-grass.

Victoria—Myrniong, Nov., 1899 (Brittlebank).

On *Poa caespitosa* Forst.—Tussock-grass.

Victoria—Kergunyah, Nov., 1902 (Robinson).

This is the well-known Rye smut, although it has not been met with naturally on this host in Australia. Through the courtesy of P. Sydow, I received fresh specimens from Germany. The spores are of a dark golden-brown colour, and 1–3 in each spore-ball are fairly common, while 4–5 are rather exceptional. The spores are either completely or often incompletely invested by sterile cells, which are generally of a yellowish tint, oblong to oval, with distended and regularly thickened walls.

Germination.—According to Brefeld[5], the spores germinate readily in water, giving rise to a longer or shorter germinal tube, and producing a whorl of 4–6 conidia at the apex. The promycelium may become septate, and the conidia grow out into long branches, septate towards the basal end.

In a nutritive solution germination occurred in a similar fashion, only the whorl of conidia grew more luxuriantly and became branched just like a mycelium.

I also germinated the spores in tap water, and the promycelium was invariably short, never longer than the conidia, and always unicellular. The cylindrical conidia formed a whorl of 3–4 at the apex, close together at first but gradually diverging. The average size was 12–15 × 3–4 μ, but sometimes they reached a length of 24 μ. Germination occurred both on a microscopic slide and floating on water in a watch-glass.

These spores were obtained from Rye plants grown in my garden, but in a previous germination I used spores obtained from Berlin. They were placed on a slide in tap-water, and they germinated freely the third day, producing a whorl of 2–6 conidia at the apex of the promycelium, which varied considerably in length, and was finally 4–5 septate.

(Plates V., LI.)

Stipa.

66. **Urocystis stipae** McAlp.

Sori in leaves, leaf-sheaths, and stems, forming elongated dark-coloured streaks, at first covered by the epidermis, but ultimately becoming free by the rupture or decay of the covering.

Spore-balls exceedingly variable in shape and size, globose, elliptical, oblong, or polygonal, light golden-brown, 22–32 μ diam., or 28–40 × 20–32 μ.

Spores round to oval, smooth, 1–5 in a ball, average 3, 12–16 × 9–12 μ; sterile peripheral cells forming a single interrupted or completely investing layer, pale-yellowish, flattened oval, 8–12 μ long.

On *Stipa luehmanni* Reader.

Victoria—Mallee, Oct., 1898 (C. French, jun.).

This species is distinct from *U. occulta*, as the spore-balls are considerably larger in size, and the individual spores are smaller.

The grass is provisionally named, as Reader states that there is a certain amount of hybridism taking place among the species of *Stipa*, and doubtless new forms will be the result, so that it is just possible that this species—*S. luehmanni*—may be reduced to a variety.

(Plate LI.)

Triticum.

67. **Urocystis tritici** Koern.

Koernicke, Hedw. XVI., p. 33 (1877).

Urocystis occulta (Wallr.) Rab. in Sacc. Syll. VII., p. 515 (1888).

Sori in leaves, leaf-sheaths, stems, and occasionally on glumes, forming elongated streaks running parallel to one another, at first covered by the raised leaden-coloured epidermis, which gradually decays in patches, allowing the escape of the black powdery spores.

Spore-balls globose, ellipsoid, or oblong, bright golden-brown, variable in size and shape, 16–40 μ diam., or 24–40 × 24–32 μ, average 32 × 24 μ.

Spores spherical or oval, 1–4 in ball, occasionally 5, 2–3 common, 9–12 μ diam., or 12–16 μ long; sterile peripheral cells generally completely investing spores, or may be only partial, very pale-yellow, ellipsoid to globose, and bulging, 9–12 μ long.

On Wheat.

Victoria—Ballarat, Dookie, Longerenong, Netherby, Rochester, Rutherglen, Tungamah, Yarrawonga, &c.

New South Wales—Common.

Queensland—Hodgson District, 1906 (Tryon).

South Australia—Common.

This species is mainly separated from *Urocystis occulta* on account of the spores from the one not infecting the other. The spores are commonly two in a ball, although three and four are also met with, and the investing layer of sterile cells is generally complete. The spore is delicately punctulate on the surface, but this is more marked in *Ur. occulta*.

Koernicke[1] had determined the smut on wheat sent from South Australia by Dr. R. Schomburgk in 1877 as a new species, *Urocystis tritici*, and according to him *Ur. occulta* is distinguished from *Ur. tritici* by the more distinctly punctulate spores, which are not generally completely invested by the sterile cells, and the sterile cells being more compressed and flattened.

Germination.—The spore germinates in water, sometimes in 24 hours, and sometimes taking a fortnight, according to the age of the spore and the season of the year. It produces a promycelium which may either be unicellular or 2–3 celled. At the apex the conidia are formed, varying from 2–6, but generally 3–4. They are at first upright and crowded together, but gradually diverge so that they stand out as finger-like processes. They are normally cylindrical, rounded at the free end, and unicellular, but may develop one or two septa. They vary in size, but are generally 12–15 μ long, and 3 μ broad.

Sooner or later the conidia, while still attached, begin to germinate at their free end, by putting forth a slender germ-tube, only about half the breadth of the conidium, and this grows out to a varying length, according to the supply of nutriment. It is filled with dense protoplasmic contents, more particularly towards the tip. These slender delicate threads, when they grow out to any considerable length, show an irregular curving, and represent the infection-threads which penetrate the young seedling, if they reach it at the proper stage of growth.

(Plates IV., V., VI., VII., LI.)

DOASSANSIA Cornu.

This genus stands higher than all the preceding in its morphological differentiation. The Peridium formed by the sterile envelope of cells which encloses the fertile spore-cluster is characteristic of the genus, and places it at the top of all known Tilletiaceae. Since the hosts are either water or bog-plants, the cortex of sterile parenchymatous cells filled with air, is evidently a contrivance to enable the spores to float, or be surrounded by water until they escape and germinate. As bearing out this idea, Brefeld[4] has observed that the envelope is most strongly developed in those species on typical water-plants, while it is less complete or only rudimentary on bog-plants. The spore-body can remain in water for a considerable time, and the spores germinate at the surface or in moist air.

The spores on germination produce an undivided germ-tube, which gives rise to a whorl of long spindle-shaped conidia. They directly produce smaller secondary conidia in various branching chains, and in a nutritive solution they form an unlimited number of aerial sprouting yeast-like conidia in direct succession.

The conidia may also give rise to hyphae which branch and again produce at various spots chains of conidia.

There is here again a clear distinction between the parasitic form producing spores which give rise to germ-tubes, each with its apical whorl of conidia, and a saprophytic form in which the conidia thus produced sprouted directly in a yeast like manner.

Australian species, 1.

Lythrum.

68. **Doassansia winteriana** (Wint.) Magn.

Magnus, Berlin, Verh. Bot. Ver. XXXII., p. 253 (1890).
Setchell, Exam. Doass. Ann. Bot. VI., p. 18 (1892).
Sacc. Syll. VII., p. 505 (1888).

Doassansia punctiformis Winter, Rev. Myc. VIII., p. 207 (1886).

Sori on both surfaces of leaf, globose, punctiform, very minute, scattered or somewhat gregarious, brownish.

Spores numerous, collected into a ball, rounded to polygonal, isodiametric, and 10–12 μ diam. or a little elongated reaching $16 \times 10{\cdot}5$ μ; epispore thin, equal, smooth, sub-hyaline; cortex composed of one layer of polygonal cells, with thick, brownish, minutely granulated walls.

On living leaves of *Lythrum hyssopifolia* L.

Victoria—Near Melbourne, Oct., 1885 (Reader).

No specimen seen.

This species was named *D. punctiformis* by Winter in 1886, but there was a *Protomyces punctiformis* determined by Niessl in 1872, which was afterwards reduced by Schroeter to *D. punctiformis* in 1887. Since Winter had given his specific name previous to Schroeter, De Toni in 1888 considered it necessary and convenient to change the name of *D. punctiformis* (Niessl) Schroet. to *D. niesslii*, and allow Winter's specific name to remain.

However, Professor Magnus considers that the specific name must be retained, independently of the genus in which the fungus is placed, and accordingly names Winter's species *D. winteriana* as above.

EXCLUDED SPECIES.

Some genera have been placed in this family whose affinities are doubtful, such as Graphiola, and Cerebella, and as the balance of evidence is against their inclusion, I have omitted them. Of course the species belonging to these genera will also be excluded

The smuts on Polygonum are rather peculiar, and it is not to be wondered at that they have sometimes been wrongly placed. The unique *Ustilago emodensis* of Berkeley was supposed to be represented in Australia, but the species mistaken for it is now shown to belong to the monotypic genus Melanopsichium.

The only other case worthy of special note is that of a supposed new species of smut found by Berkeley on maize. He named and described it as *Tilletia epiphylla*, although he observed its rust-like character, but a careful examination of a portion of the original material shows that it is a well-known rust.

It is rather interesting to observe that the first determination of this species was the correct one, for Mr. Bailey, F.L.S., Colonial Botanist of Queensland, wrote to me as follows, in 1893:—"In the year 1878 the maize about Brisbane was infested with a Uredo, which Messrs. Berkeley and Broome determined to be *Uredo maydis* DC. After this, these two specialists found this maize fungus to be a new Tilletia, and described it as *Tilletia epiphylla* B. and Br."

1. **Ustilago cesatii** F. v. W. = *U. rabenhorstiana* Kuehn, the name given by Cooke in his Handbook to the smut occurring on *Paspalum scrobiculatum*, but on examining a portion of the original material forwarded to Cooke, it is found to be a Sorosporium, and is now named *S. paspali*.

2. **Ustilago destruens** Schlecht. is given by both Cooke and Massee as occurring on native species of Danthonia, but an examination of portions of the original material shows that it is a different and, in fact, a new species, *Ustilago readeri* Syd.

U. destruens Schlecht. is considered to be a synonym of *U. panici-miliacei* (Pers.) Wint., and since this has been determined as a Sorosporium, the distinction from the one occurring on Danthonia is decided.

Sorosporium panici-miliacei (Pers.) Takash. has been found on species of Panicum, so that it is only excluded here from being wrongly determined on Danthonia.

3. **Ustilago emodensis** Berk.—I have received some of the original material from Queensland through the courtesy of Bailey, and find that the spores are developed in cavities in the tissues of the stem, so that it belongs to the genus *Melanopsichium* Berk.

4. **Ustilago zeae** (Beckm.) Unger=*U. maydis* Corda.—The smut occurring on Maize in Australia was naturally considered to be the common American Corn Smut, and Dr. Cobb recorded it as such, but the examination of a large number of specimens from different States showed it to be the Head Smut. This smut generally confines itself to the inflorescence, hence the name, and does not attack the leaves or stem, forming smut-balls, like the other, It is quite a distinct genus, and the constant repetition of the original error renders it necessary to emphasize the fact that the common Corn Smut of America has not hitherto been found in Australia.

5. **Tilletia epiphylla** B. and Br.—I am indebted to Bailey for a portion of the type specimen, and at first sight it certainly looks like a rust with its gregarious minute pustules. On examining the spores this suspicion is found to be correct, as they are provided with 2–3 equatorial germ-pores on one face, as shown in the photograph. (Plate L., Fig. 183). From its size, colour, and markings it evidently belongs to *Puccinia maydis* Bereng. The original specimen was sent to Berkeley, who determined it as a new species of Tilletia, giving the size of the spores as 36 μ diam., but he evidently observed its rust-like character for he remarks—"*Uredo maydis* DC., is a much larger plant, with much smaller spores.

Then Massee[2] in *A Revision of the genus Tilletia* gives the result of his examination of the type specimen. He found the spore, instead of being smooth " to be studded at regular intervals with very minute warts," and concludes that—" the gregarious, small, linear pustules resemble a *Puccinia* superficially." If he had only observed the germ-pores it would have shown that there was more than a superficial resemblance.

6. **Graphiola phoenicis** (Moug.) Poit.—This genus, with its most commonly occurring species found on palm leaves in Queensland, is now generally excluded from the Smuts, although its systematic position has not been determined.

7. **Cerebella** Ces.—This genus, occurring in Queensland, with its two species *C. paspali* Cooke and Mass. on *Paspalum scrobiculatum* L., and *Anthistiria ciliata* L. f. and *C. andropogonis* Ces. on *Heteropogon contortus* R. and S.—is now placed among the Hyphomycetes by Prof. Saccardo.

EXPLANATION OF TERMS.

Abstriction.—The formation of a spore by pinching off the end of a spore-forming hypha.
Aecidiospore.—A spore formed in an aecidium, being produced in chains from the hymenium lining the internal surface.
Aecidium.—The usually cup-shaped envelope within which aecidiospores are produced.
Alien.—An introduced plant which has become naturalized.
Amphimixis.—The intermingling of the properties of the two sex-cells in the process of fertilisation, when they are clearly distinct.
Anastomosis.—The union of hyphae by numerous cross-connexions, forming an irregular network.
Anti-toxin.—A secretion which neutralizes or counteracts the effects of a toxin or poisonous secretion.
Ascomycetes.—A group of fungi in which the spores are produced by free-cell formation in a mother cell or ascus.
Ascus.—The spore mother-cell, which is usually the swollen end of a hypha.
Autobasidium.—An undivided basidium, consisting of a single large cell.
Basidiomycetes.—A group of fungi producing spores on basidia.
Basidium.—A terminal tubular cell, bearing at its apex a definite number of spores or conidia, usually four; or divided transversely, and each cell giving rise to a reproductive body.
Basipetal.—Applied to conidia or spores when the youngest of a chain are produced at the base.
Bunt.—A common name applied to Stinking Smut of wheat.
Cereal.—Any of the grasses whose grains serve as food.
Chemotaxis or *Chemotropism.*—A form of sensitiveness which certain organisms possess towards particular chemical substances.
Chlamydospore.—A thick-walled resting-spore.
Chlorophyll.—The green colouring matter of plants, which enables the chlorophyll grains to utilize inorganic food.
Conidium.—A reproductive cell asexually produced and arising by a process of budding.
Conjugation.—The fusion of sexual elements, the two uniting elements or gametes being similar.
Contagion.—The transmission of disease by direct contact of the part affected with the disease.
Dominant.—Applied to such characters arising in the crossing of two individuals as prevail and assert themselves over contrasted characters which are kept in the background.
Echinulate.—Covered with short spines.
Endospore.—The innermost coat of a spore.
Exospore.—The outer covering of a spore
Fertilisation.—The union of two germ-cells derived from male and female organisms respectively and becoming physiologically one.
Fungi.—Plants destitute of chlorophyll, and without the systems of tissues characteristic of higher plants, but may be unicellular or composed of more or less compacted strands of cells or hyphae.
Fungicide.—Any substance which acts injuriously to fungi or destroys them completely.
Gall.—A monstrous growth or morbid enlargement of the cells of a plant, due to parasitic agency.
Gametes.—Germ-cells derived from male or female organisms, that from the male being known as spermatozoon or sperm cell, and that from the female as ovum or egg-cell.
Gametophyte.—The stage in the life-cycle of a plant which bears the sexual organs.
Germinal tube.—A tubular process from a spore developing into a promycelium.
Germ-tube.—A tubular process from a spore or conidium developing into a hypha, and ultimately into a mycelium.
Haustorium.—A short lateral branch of a hypha, penetrating a cell of the host-plant, and acting as a sucker as well as an organ of attachment.
Hemibasidia.—A term applied by Brefeld to the promycelia of the Smuts, as they show their primitive nature by being divided and bearing a variable number of conidia.
Heredity.—"The genetic relation between successive generations," or "The transference of similar characters from one generation of organisms to another, a process effected by means of the germ-cells or gametes."
Host or Host-plant.—A plant which nourishes a parasite.
Hyaline.—Colourless or translucent.
Hymenium.—A spore-bearing layer of hyphae.
Hypha.—A tubular thread-like structure, collectively constituting the vegetative body or mycelium of the fungus.

Immunity.—The absence of susceptibility to an infectious disease, even although the germ-tube of the parasitic fungus has entered the host-plant, without, however, multiplying therein and producing disease.

Incubation-period.—The time which elapses between the introduction of the infective tube and the production of the characteristic fungus.

Indigenous.—Native to a country and not introduced, at least within the historic period.

Infection.—The introduction of a living micro-organism or the germ-tube of a parasitic fungus into the host-plant, where it multiplies and produces disease.

Inflorescence.—The arrangement of several flowers on a common axis, and in grasses the axis or stalk is known as the Rachis.

Inoculation.—The entrance of the germ-tube of the parasitic organism into the host-plant, irrespective of the causation of disease.

Intercellular.—Between the cells of the host-plant.

Intracellular.—Within the cells of the host-plant.

Lumen.—The cavity bounded by the walls of an organ, as the central cavity of a cell.

Metabolism.—The sum of the chemical changes in a living cell.

Micron or *Micromillimetre.*—The standard unit for microscopical measurements equalling 1-1000th of a millimetre, or 1-25000th of an inch, and indicated by the sign μ.

Mycelium.—The vegetative portion of a fungus composed of hyphae.

Nucleus.—An organized proteid constituent of the cell, playing an important part in its nutritive and reproductive processes.

Oospore.—The fertilised ovum or egg-cell.

Ovary.—That portion of the female organ of a flowering plant which contains the ovules.

Parasite.—An organism living on or in another living organism and at its expense.

Pathology.—The science of disease. Vegetable Pathology is that division of it which treats of plant diseases.

Peridium.—The enveloping layer enclosing spores as in the Puff-balls and the aecidium of the Rusts.

Phycomycetes.—A group of fungi which are alga-like in their characters, with sexual and asexual reproduction.

Predisposition.—The tendency to disease exhibited by an organism when the conditions are favorable to the development of the parasite.

Promycelium.—Applied to the germinal tube produced by the spore of the Rusts and Smuts.

Pronucleus.—The nucleus of a conjugating gamete which unites with another pronucleus to form the germ-nucleus.

Protobasidium.—A basidium transversely divided and consisting of several cells.

Protoplasm.—The living substance of which animals and plants are composed.

Pseudomixis.—The union of the sexual cells in the process of conjugation, when they are approximately equal.

Pulverulent.—Powdery, applied to spores when they are dusty and not agglutinated together.

Rachis.—The axis or stalk in the inflorescence of grasses.

Recessive.—Applied to such contrasted characters, arising in the crossing of two individuals, as are kept in abeyance or apparently suppressed, at least, in the first generation.

Saprophyte.—A fungus which preys upon dead organic matter only, in contrast to a parasite.

Septate.—Partitioned off into distinct divisions.

Septum.—A partition or cross-wall.

Sorus.—A cluster of spores constituting a spore-bed.

Spore.—A detachable cell capable of reproducing the fungus.

Sporidium.—A spore abjointed from a promycelium, equivalent to a conidium. Sporidiolum is the term proposed by Saccardo, since sporidium is already applied to an ascospore.

Sporophyte.—The stage in the life-cycle of a plant which bears the spores.

Stigma.—The top of the pistil upon which the pollen is received.

Stroma.—Fungus body in the form of a cushion or expansion, bearing reproductive bodies.

Symbiosis.—The living together of dissimilar organisms which mutually help and support each other.

Teleutospore.—Generally regarded as the ultimate spore in the life-cycle of the Rusts which germinates and produces a promycelium. Sometimes also applied to the spore of the Smuts.

Toxin.—A poisonous secretion of certain Fungi which kills the cells of the host-plant and prepares the way for the entrance of the parasite.

Unicellular.—Consisting of a single cell.

Uredospore.—A spore detached from the apex of a pedicel and producing a mycelium which bears uredospores or teleutospores or both.

Vacuole.—A space in the protoplasm of cells which contains a watery fluid, the cell-sap.

Verrucose.—Warty, covered with small warts.

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G. H. Robinson, Phot. Nat. Size.

HEAD SMUT OF WHEAT GRASS

(*Ustilago Bullata.*)

G. H. Robinson, Phot. Nat. Size.

GALL SMUT OF BARNYARD GRASS

(*Cintractia Crus-Galli.*)

G. H. Robinson, Phot.

Nat. Size.

SMUT OF COUCH GRASS

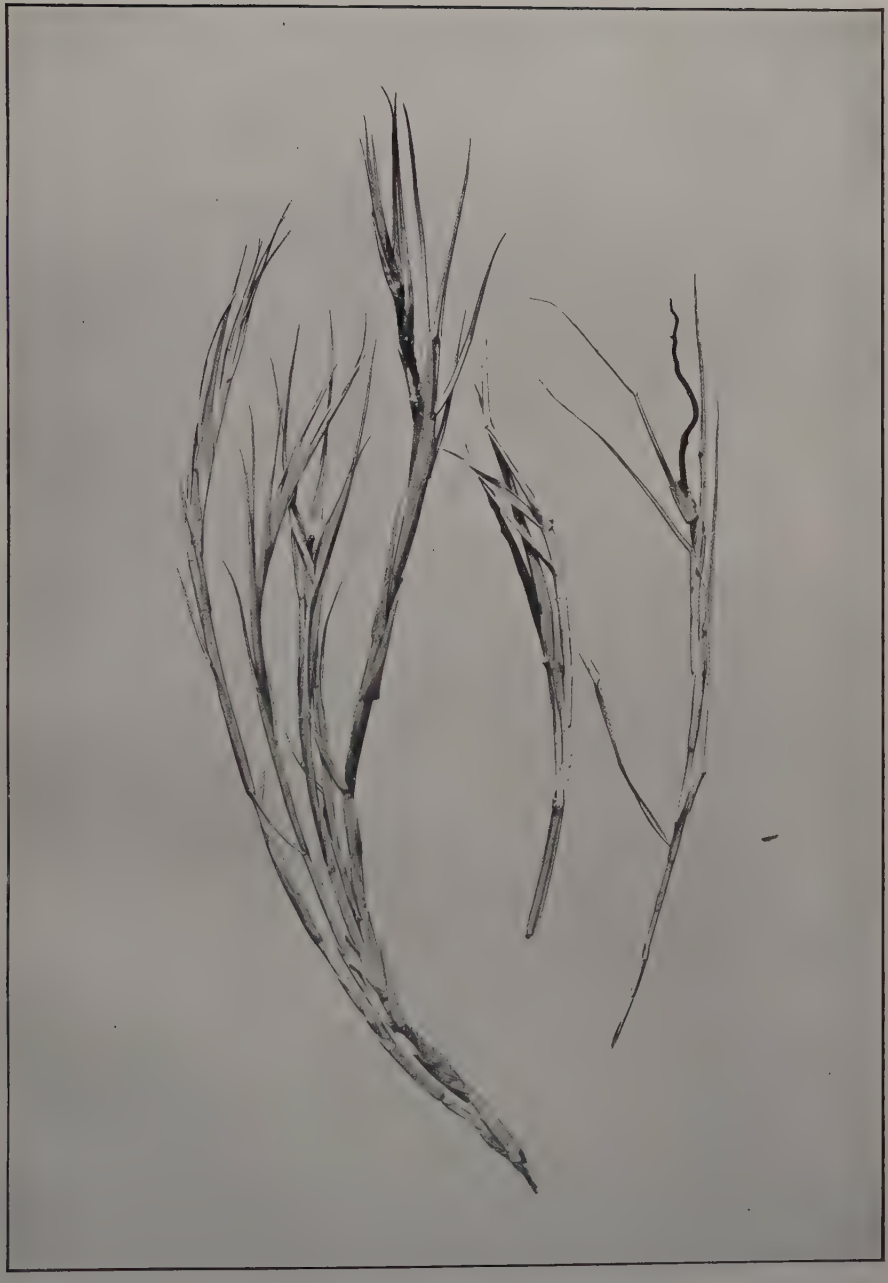
(*Ustilago Cynodontis.*)

G. H. Robinson, Phot.

Nat. Size

SMUT OF MAT GRASS

(Cintractia Densa.)



G. H. Robinson, Phot.

Nat. Size.

SMUT OF COAST GRASS

(*Cintractia Distichlydis.*)

G. H. Robinson, Phot.

Nat. Size.

BALL SMUT OF WATER GRASS

(Sorosporium Solidum.)

PLATE XXVI.

(*All Figures* × 500 *unless otherwise stated.*)

USTILAGO.

Fig.

1. Spores of *U. avenae.*

2. Spore-germination of *U. avenae* in water (after Brefeld) × 450. The upper row shows the formation of conidia. The lower row is an older stage, where the formation of conidia has ceased, and the spore at the end shows a "buckle joint," *i.e.*, one segment of the promycelium becomes connected with another by means of a curved tube.

3. Spore-germination of *U. avenae* in nutritive solution, showing the luxuriant formation of conidia (after Brefeld) .. .. × 200

4. Germinating spore of *U. avenae* forming a buckle joint.

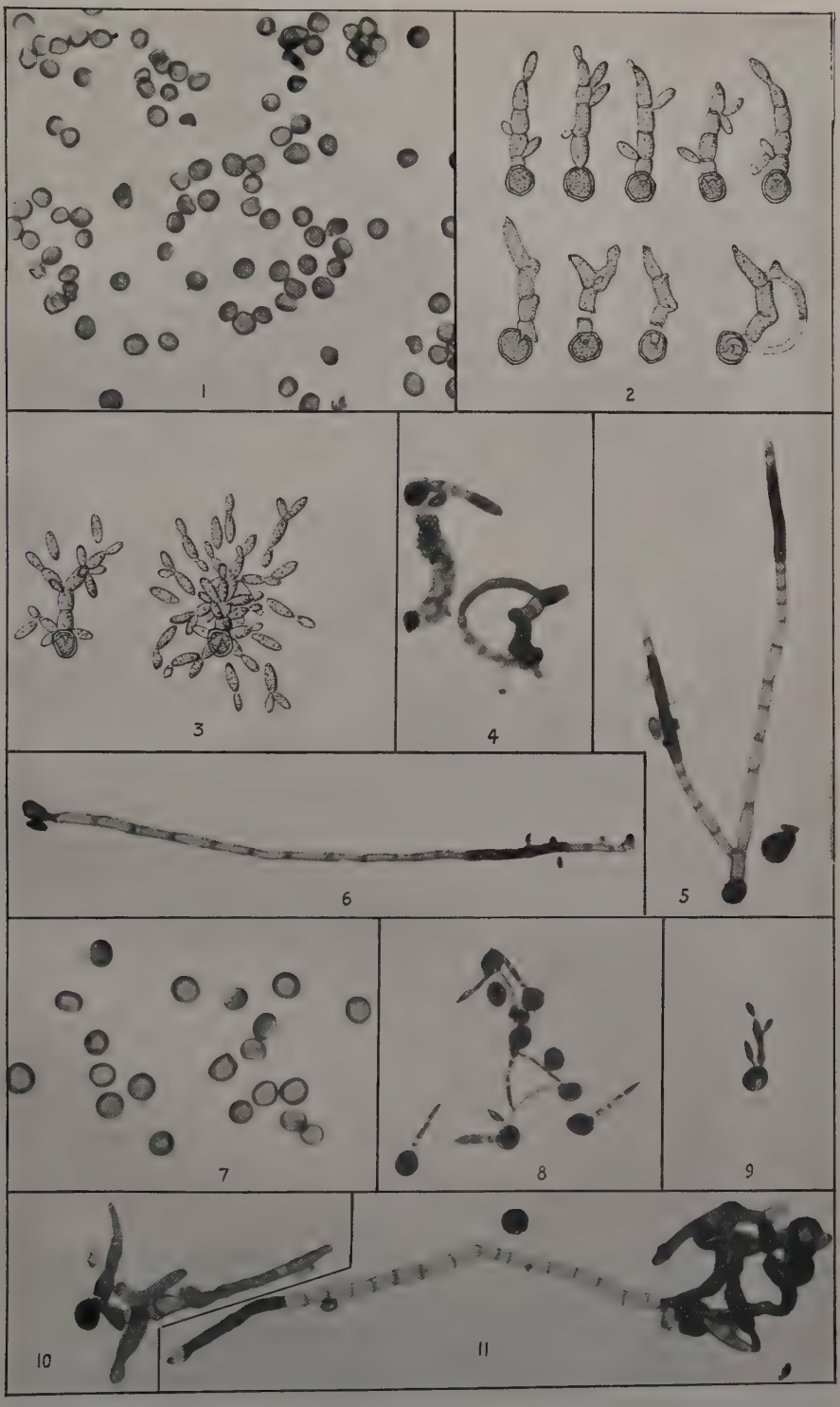
5. Germinating spore of *U. avenae* emitting a long branched septate tube instead of the ordinary promycelium.

6. Germinating conidium of *U. avenae.*

7. Spores of *U. hordei.*

8, 9. Germinating spores of *U. hordei,* with conidia.

10, 11. Spores of *U. hordei* germinating and forming branching septate elongated tubes.



G. H. Robinson, Phot.

× 200, 450, and 500.

USTILAGO.

PLATE XXVII.

(*All Figures* × 500 *unless otherwise stated.*)

USTILAGO.

Fig.

12. Strongly developed branched germinal tube from spore of *U. hordei.*

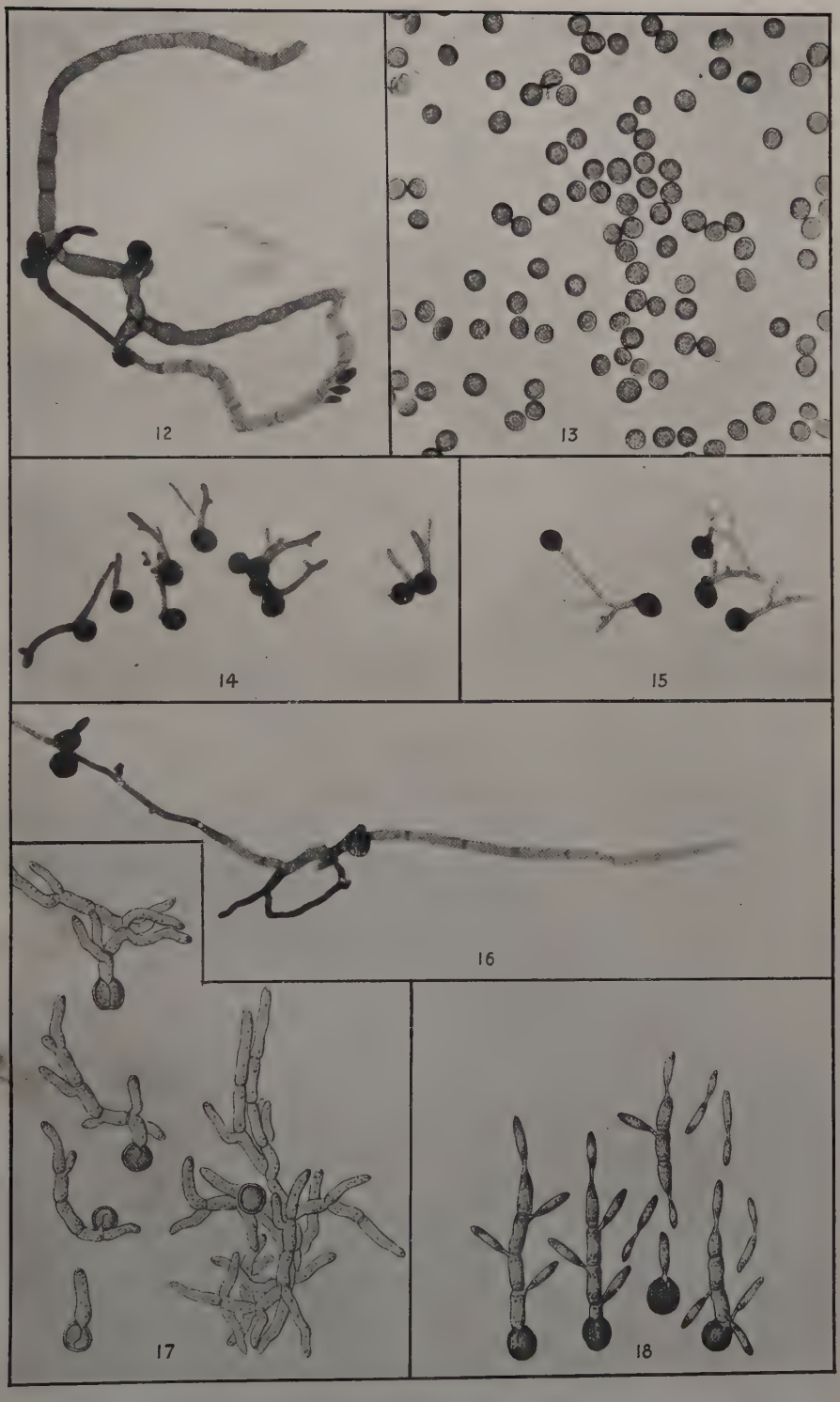
13. Spores of *U. nuda.*

14, 15. Germinating spores of *U. nuda.*

16. Strongly developed germinal tube from spore of *U. nuda.*

17. Germinating spores of *U. nuda*, showing different stages of development of the germinal tube (after Brefeld) .. .. × 350

18. Spore germination of *U. hordei* in a nutritive solution (after Brefeld) .. × 350



G. H. Robinson, Phot.

× 350 and 500.

USTILAGO.

PLATE XXVIII.

(*All Figures* × 500 *unless otherwise stated.*)

USTILAGO.

Fig.

19. Spores of *U. tritici.*

20, 21. Germinating spores of *U. tritici,* showing typical curved germinal tubes.

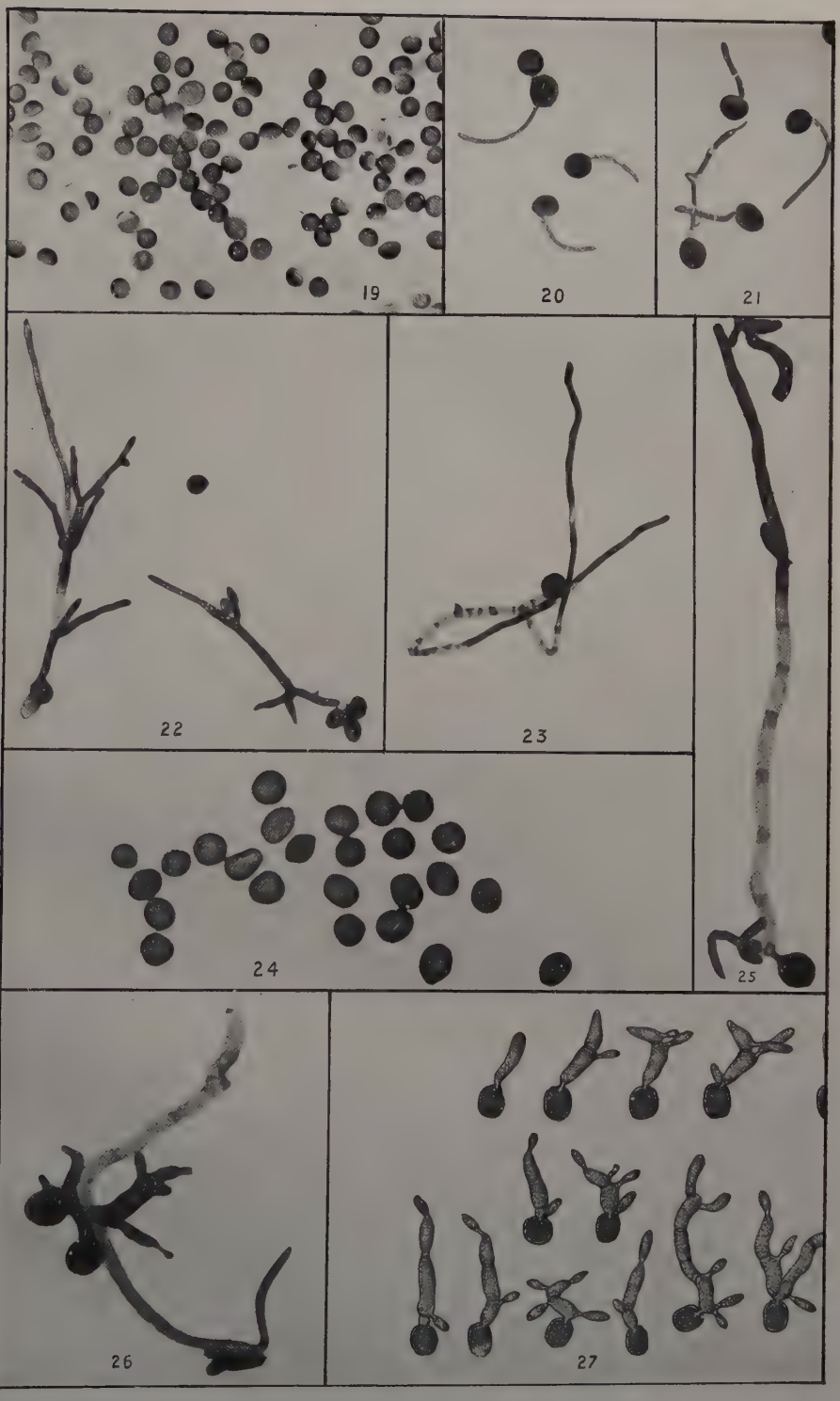
22, 23. Strong growth from spores of *U. tritici* after being four days in water.

24. Spores of *U. bromivora.*

25. Germinating spores of *U. bromivora* after 48 hours in hay infusion. Promycelium giving rise to conidia and one extremely long septate tube.

26. Two germinating spores of *U. bromivora,* one with conidia forming.

27. Spore germination of *U. bromivora* in nutritive solution (after Brefeld) — × 400



G. H. Robinson, Phot.

× 400 and 500.

USTILAGO.

PLATE XXIX.

(*All Figures* × 500 *unless otherwise stated.*)

USTILAGO.

Fig.

28. Spores of *U. bullata.*

29. Germinating spores of *U. bullata.*

30. Germinating spores of *U. bullata* (after Brefeld) × 350. The two spores producing two and three germinal tubes respectively, but no conidia were germinated in water. The others were germinated in nutritive solution, and show not only the formation of conidia, but one conidium sproutin in a veast-like manner, and another producing a filament at both ends.

31. Spores of *U. calandriniae.*

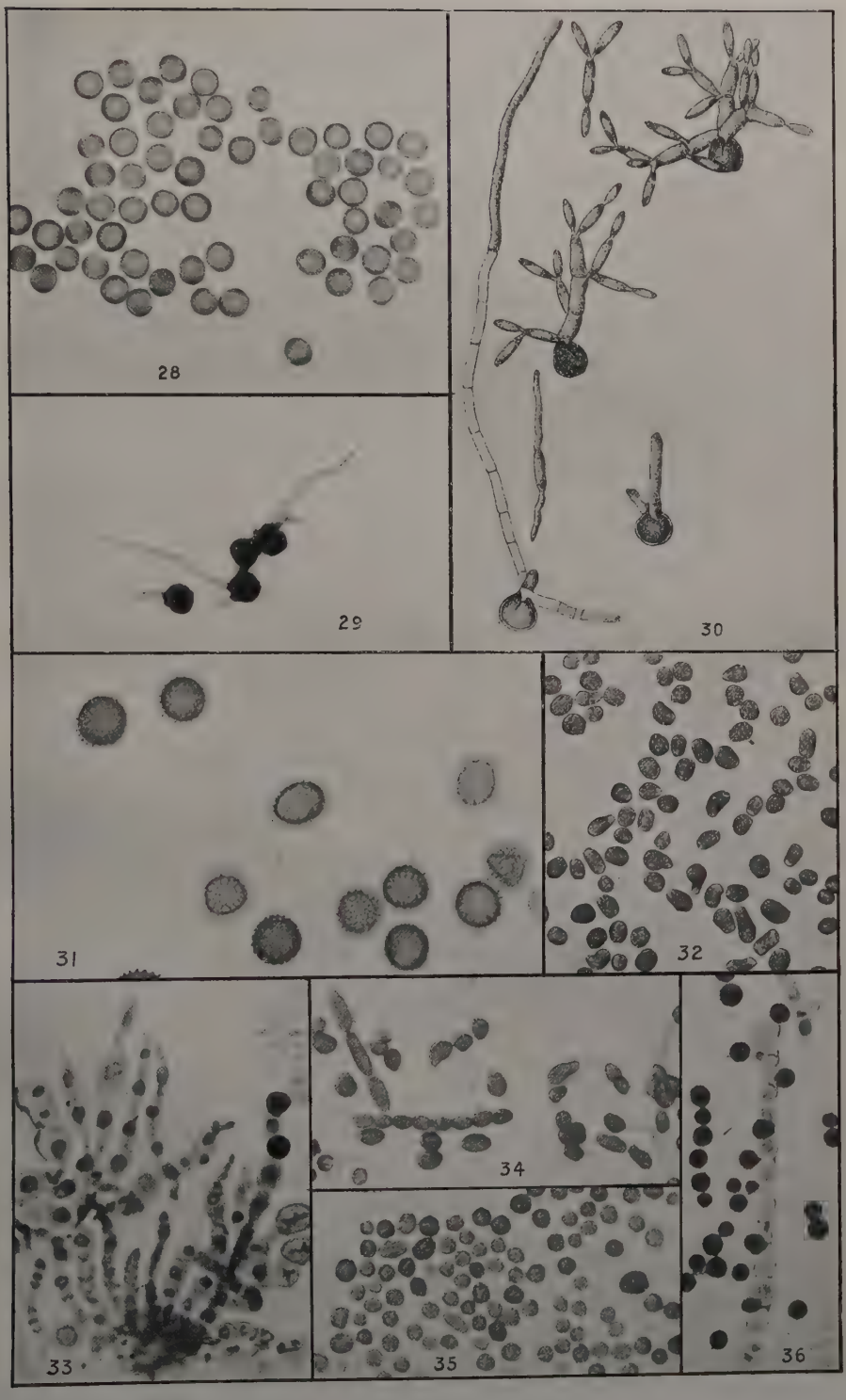
32. Spores of *U. olivacea* from original material from Ludwig.

33. Spore-forming hyphae from same.

34. Spores of *U. olivacea* from Tasmanian material.

35. Spores of *U. olivacea* from Sydow's Ustilagineen, No. 357.

36. Spores and spore-bearing mycelium of *U. olivacea* from preceding.



G. H. Robinson, Phot.

x 350 and 500.

USTILAGO.

PLATE XXX.

(*All Figures* × 500 *unless otherwise stated.*)

SOROSPORIUM REILIANUM.

Fig.

37. Spore-balls from a very young smutted cob of maize .. .. .. × 250

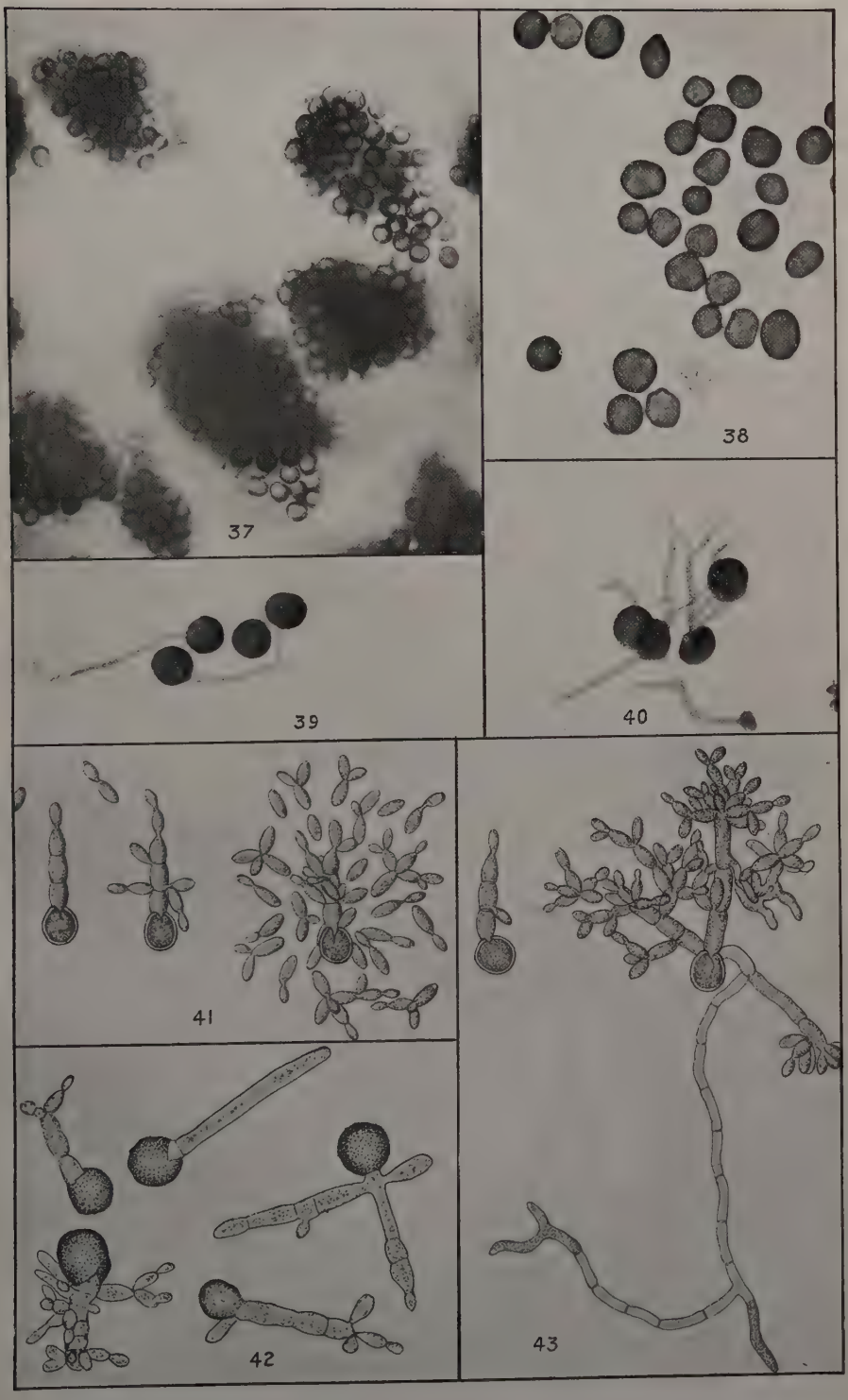
38. Spores.

39, 40. Germinating spores, with formation of conidia.

41. Spore germination in nutritive solution (after Brefeld) × 350. The successive development of the germination shown, the conidia finally becoming detached, and sprouting in a yeast-like manner so as to form small colonies.

42. Germination of spores after three days in water (after Norton) ... ... × 600

43. Spore germination in nutritive solution from another culture (after Brefeld) × 350 The spore on the right has produced three germinal tubes, bearing numerous conidia, some of which have formed germ-tubes while still attached.



G. H. Robinson, Phot.

x 250, 350, 500, and 600.

SOROSPORIUM REILIANUM.

PLATE XXXI.

(*All Figures* × 500 *unless otherwise stated.*)

USTILAGO.

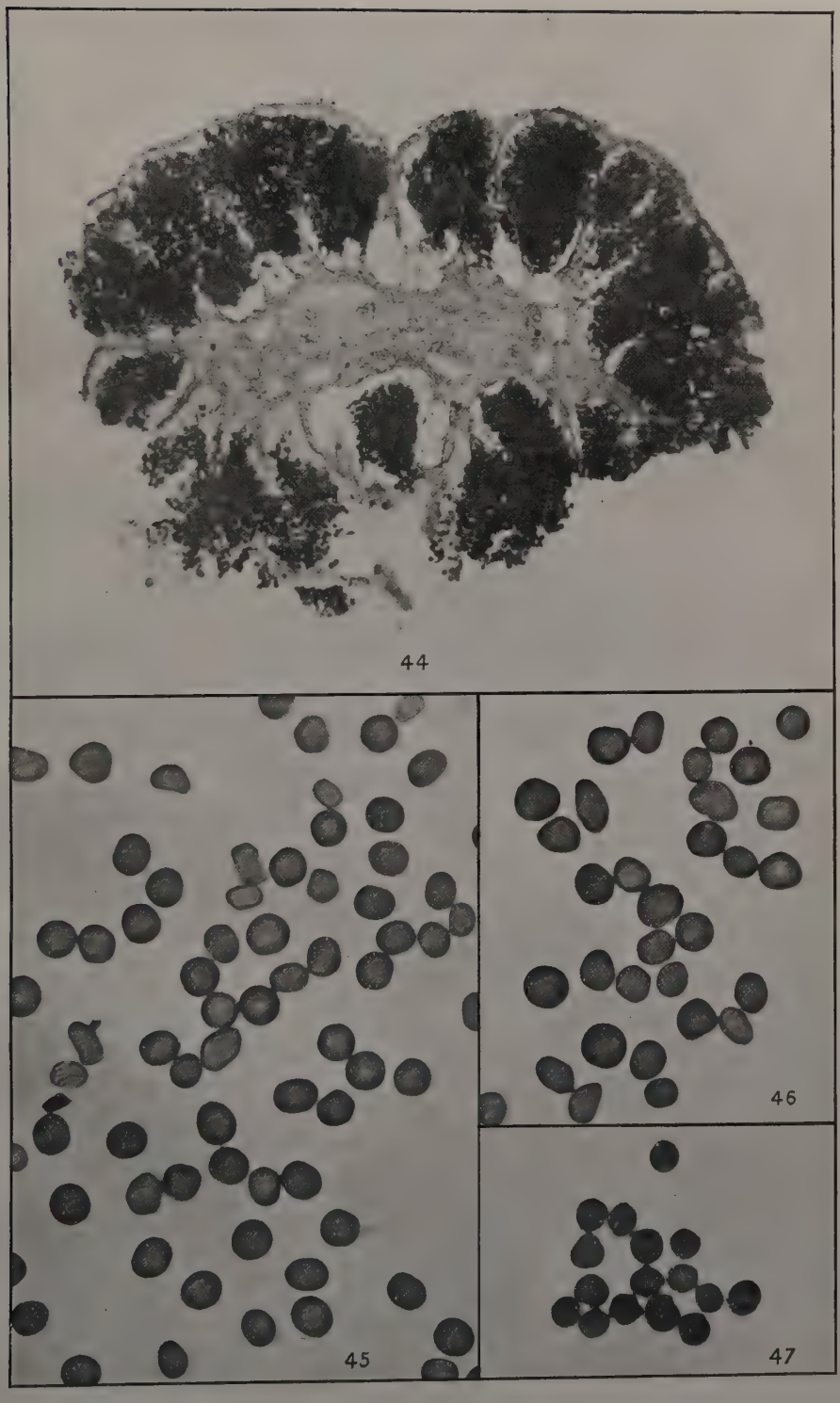
Fig.

44. Section through axis of inflorescence of *Danthonia penicillata* affected with *U. readeri* .. .. × 100

45. Spores of *U. readeri* on same, being part of specimen from Ludwig, labelled *U. leucoderma* Berk.

46. Spores of *U. readeri* from *Danthonia semiannularis.*

47. Spores of *U. hieronymi* from *Triodia mitchelli.*



G. H. Robinson, Phot.

× 100 and 500.

USTILAGO.

PLATE XXXII.

(*All Figures* × 500 *unless otherwise stated.*)

USTILAGO AND CINTRACTIA.

Fig.

48. Spores of *Cintractia spinificis* from *Spinifex hirsutus.*

49. Spores of *U. stenotaphri* from *Stenotaphrum americanum.*

50, 51. Spores of *U. utriculosa.* Surface view showing the reticulated markings.

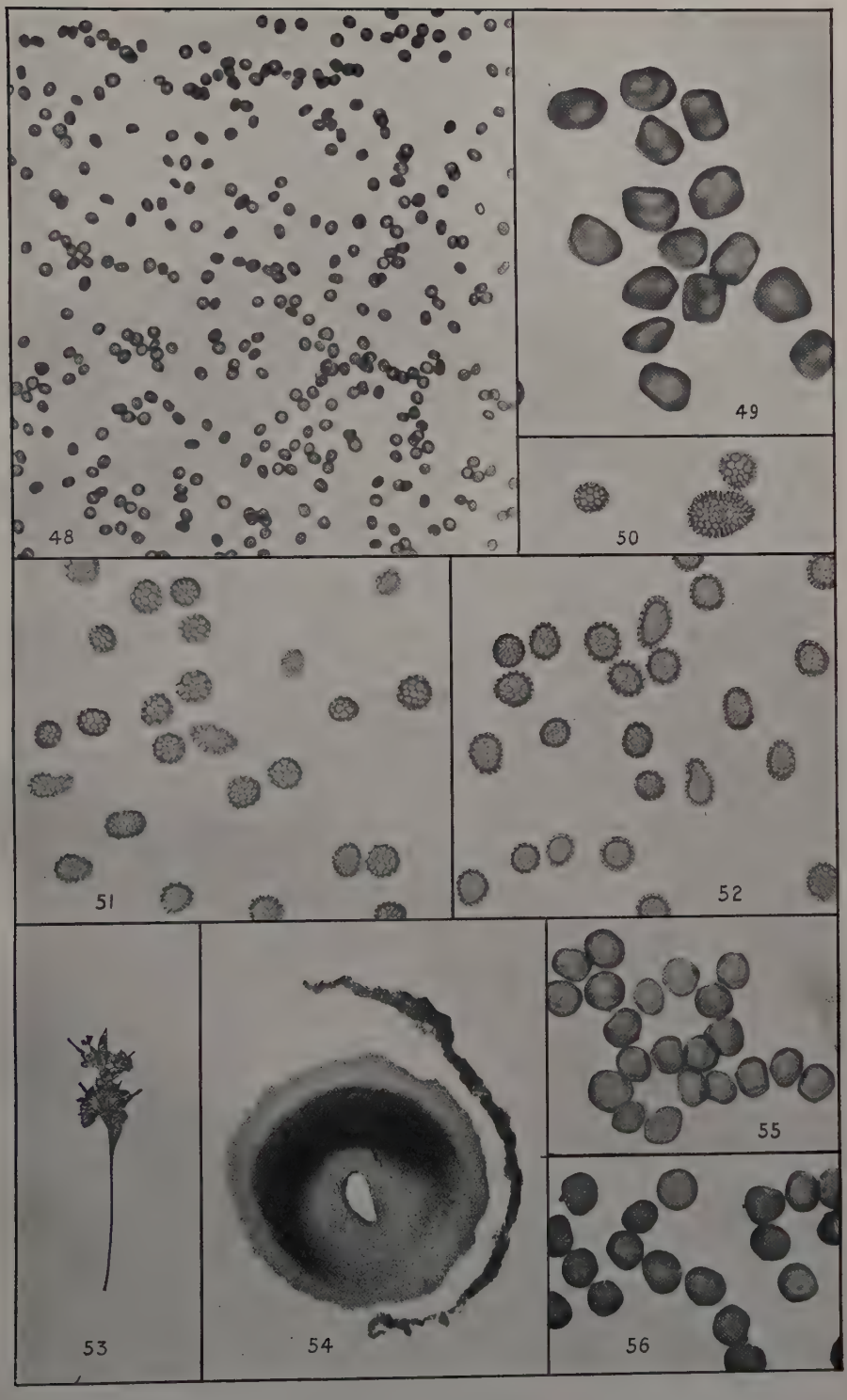
52. The same, sectional view.

53. Portion of inflorescence of Polygonum affected by *U. hydropiperis* var. *columellifera* Tul. Note the black columella projecting from each floret .. nat. size

54. Section towards base of columella of same. The dark crescent-shaped portion represents the nearly-mature spores, the paler portions the immature spores in process of formation .. .. × 20

55. Spores of same on Polygonum from Tasmania.

56. Spores of *U. hydropiperis* from Rabenhorst's Fungi Europaei, No. 2390.



G. H. Robinson, Phot.

Nat. Size, and x 20 and 500.

USTILAGO AND CINTRACTIA.

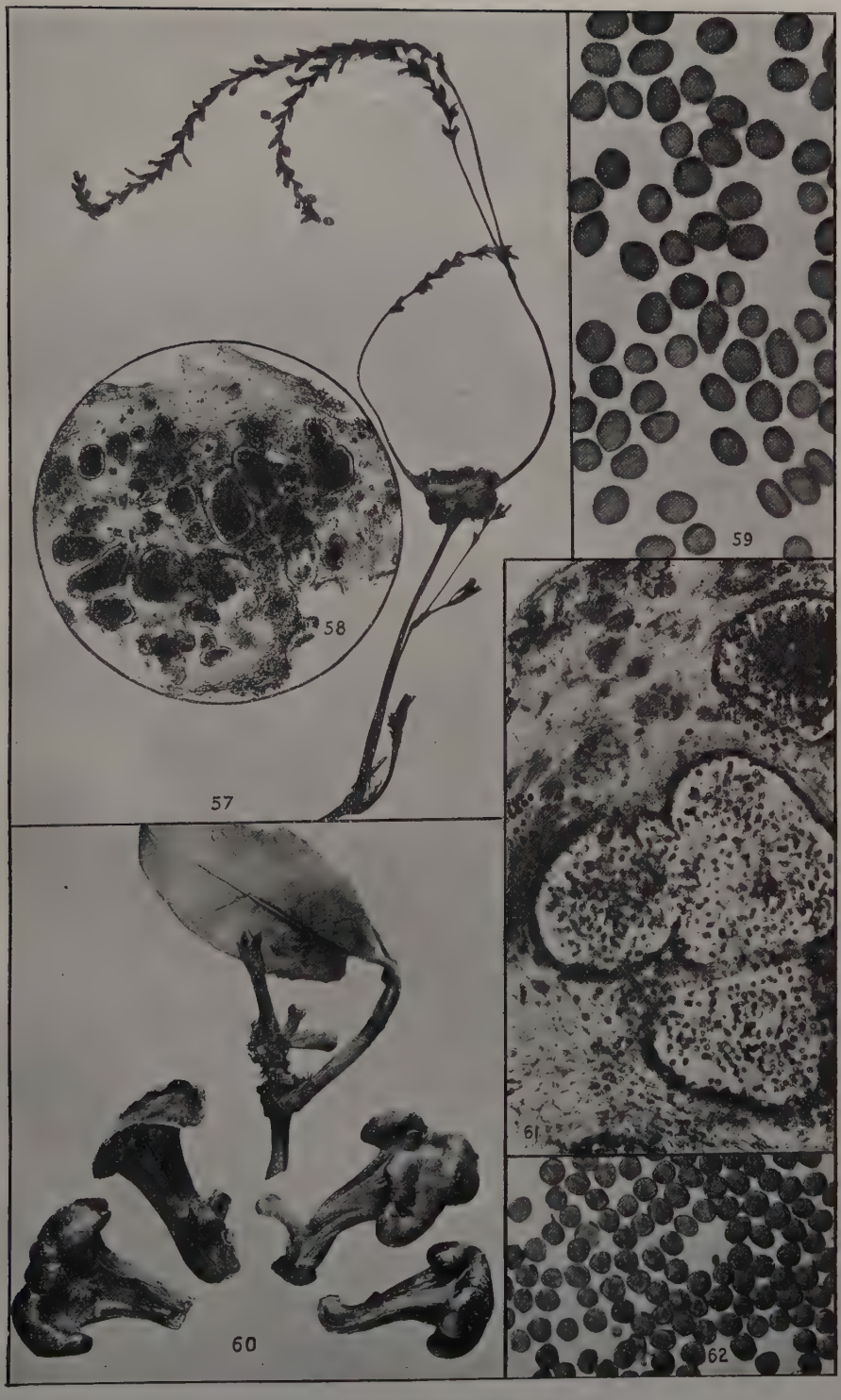
PLATE XXXIII.

(*All Figures* × 500 *unless otherwise stated.*)

MELANOPSICHIUM.

Fig.

57. Stem of Polygonum showing gall due to *M. austro-americanum* .. .. nat. size
58. Section through gall, showing the distorted and enlarged cells containing spores × 20
59. Spores of above.
60. Galls of *U. emodensis* on Polygonum from Java .. .. .. nat. size
61. Section of gall of *U. emodensis* .. .. × 100
62. Spores of *U. emodensis*.



G. H. Robinson, Phot.

Nat. Size, and × 20, 100, and 500.

MELANOPSICHIUM.

PLATE XXXIV.

(*All Figures* × 500 *unless otherwise stated.*)

USTILAGO AND CINTRACTIA.

Fig.

63. Section through axis of inflorescence of Stipa affected by *C. hypodytes* .. × 25

64. Portion of a similar section .. .. × 150

65. Spores of same.

66. Section through portion of axis of inflorescence of *Cynodon dactylon* affected by *Ustilago cynodontis* .. .. × 100

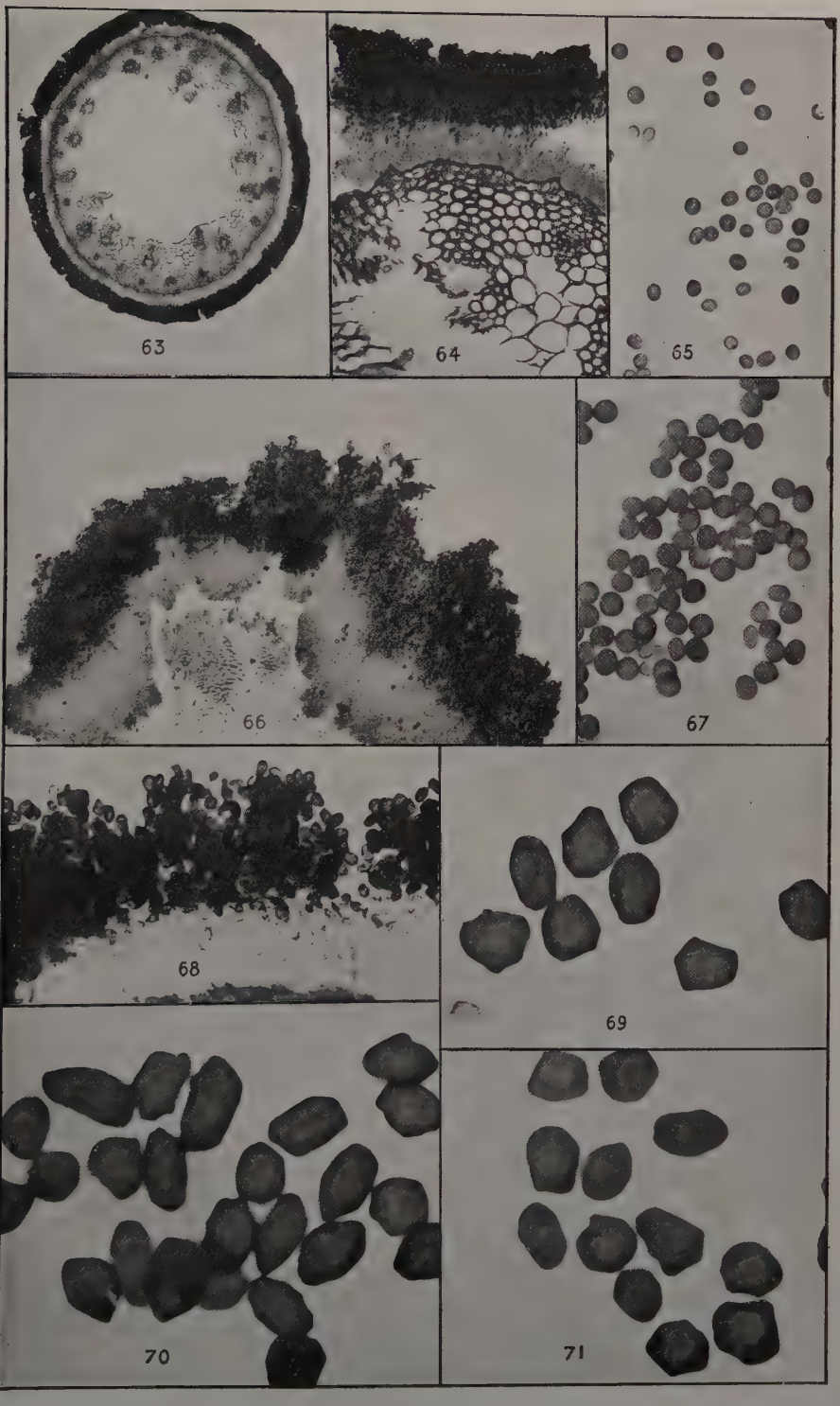
67. Spores of *U. cynodontis.*

68. Section through ovary of *Carex breviculmis* affected by *C. caricis* .. × 150

69. Surface view of spores from above, showing markings.

70. Sectional view of spores.

71. Spores of *C. caricis* from Sydow's Ustilagineen, No. 360.



G. H. Robinson, Phot.

x 25, 100, 150, and 500.

USTILAGO AND CINTRACTIA.

PLATE XXXV.

(*All Figures* × 500 *unless otherwise stated.*)

CINTRACTIA CRUS-GALLI.

Fig.

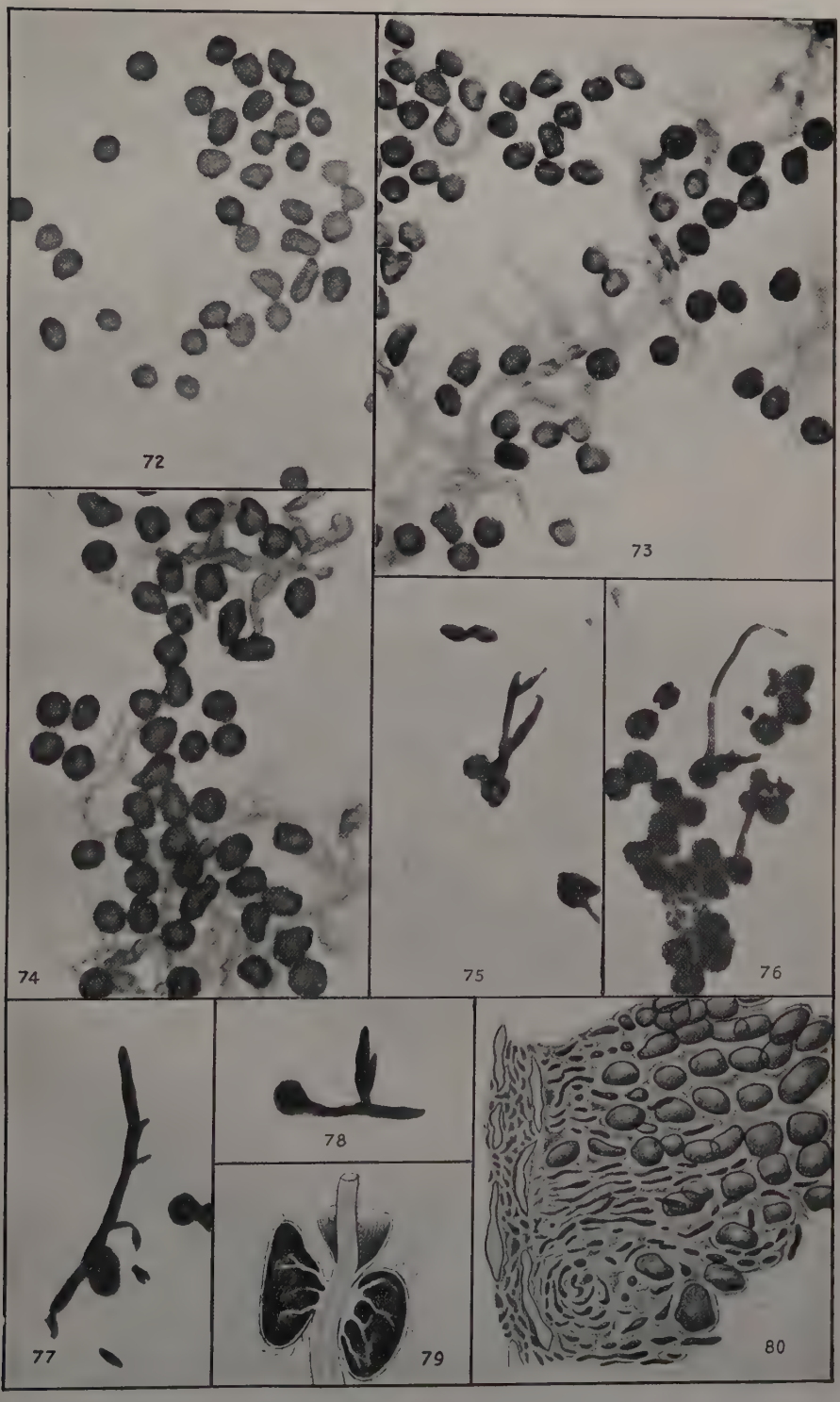
72. Spores from *Panicum crus-galli.*

73, 74. Spores and mycelium of the same.

75, 76, 77, 78. Germinating spores of the same.

79. Longitudinal section through two swellings caused by the smut on an internode of the stem. The hairy epidermis is seen covering the smut, and plate-like branching outgrowths pass from the stem into the pustule (after Magnus) .. .. enlarged

80. Transverse section through the base of the pustule, showing the formation of spores. The spores are in rows, the youngest towards the base, and hyphae with elongated segments between the rows (after Magnus) .. × 750



G. H. Robinson, Phot.

Enlarged, x 500 and 750.

CINTRACTIA CRUS-GALLI.

PLATE XXXVI.

(All Figures × 500 *unless otherwise stated.)*

CINTRACTIA.

Fig.

81. Section through axis of inflorescence of *Distichlis maritima* affected by *C. distichlydis* .. .. × 25

82. Portion of similar section enlarged .. .. × 150

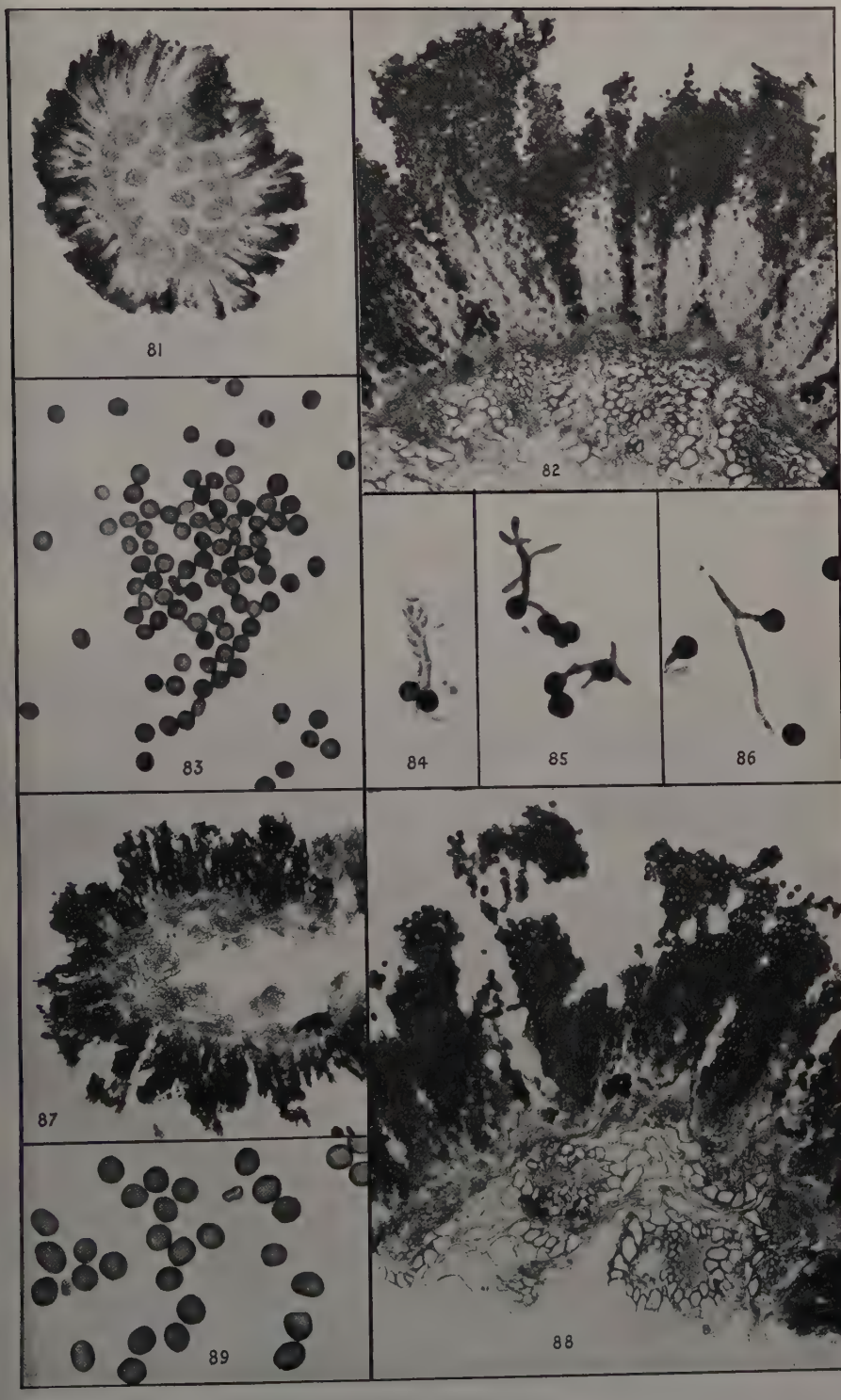
83. Spores of same.

84, 85, 86. Germinating spores of same.

87. Section through axis of inflorescence of *Rottboellia compressa* affected by *C. densa* .. .. × 50

88. Portion of similar section enlarged .. .. × 150

89. Spores of same.



G. H. Robinson, Phot.

× 25, 50, 150, and 500.

CINTRACTIA.

PLATE XXXVII.

(*All Figures* × 500 *unless otherwise stated.*)

USTILAGO AND CINTRACTIA.

Fig.

90. Section through axis of inflorescence of *Danthonia pilosa* affected by *U. comburens* .. .. × 50

91. Similar section enlarged .. .. × 100

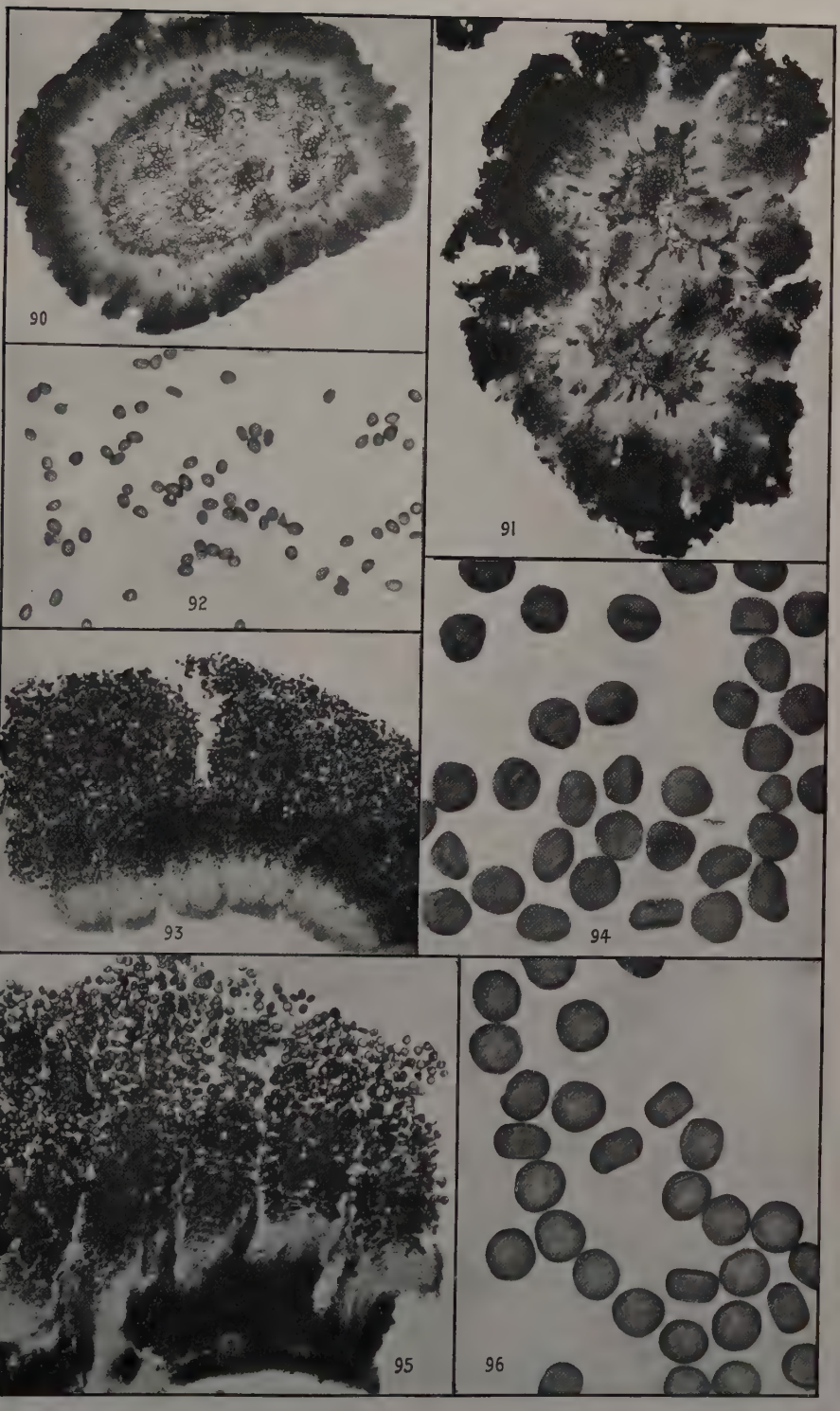
92. Spores of same.

93. Section through stroma of *C. leucoderma* on *Rynchospora aurea* .. .. × 50

94. Spores of same.

95. Section through stroma of *C. axicola* on Fimbristylis .. .. × 50

96. Spores of same.



G. H. Robinson, Phot. × 50, 100, and 500.

USTILAGO AND CINTRACTIA.

PLATE XXXVIII.

(*All Figures* × 500 *unless otherwise stated.*)

CINTRACTIA EXSERTA.

Fig.

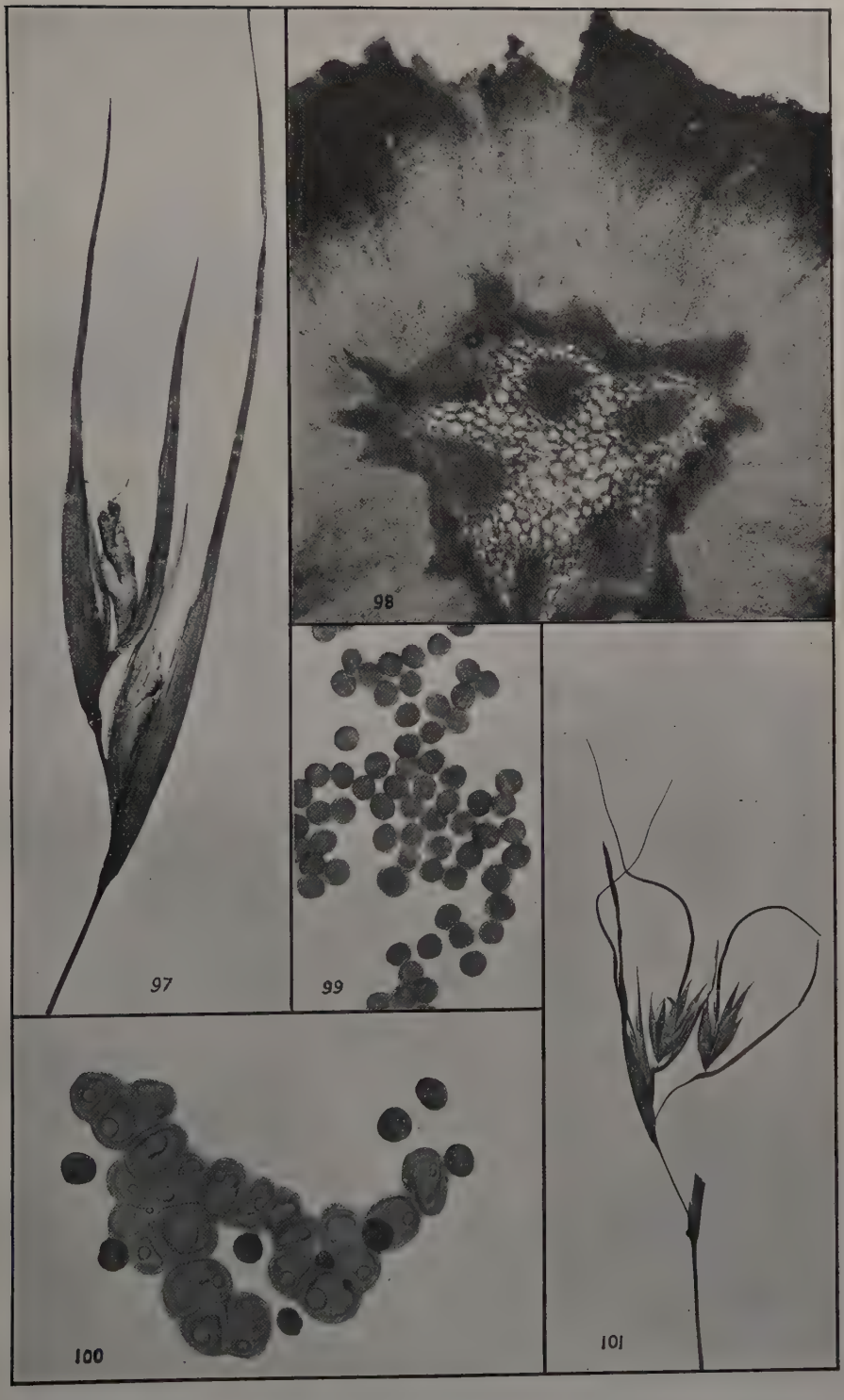
97. Portion of inflorescence of *Anthistiria ciliata* affected by *C. exserta*, showing the distortion produced and the total absence of any vestige of the awn (compare Fig. 101) .. .. × 2

98. Section through axis of inflorescence affected by *C. exserta* .. .. × 100

99. Spores of *C. exserta.*

100. Sterile fungus cells in chains, with walls thickened, and hyaline.

101. Portion of normal inflorescence of *Anthistiria ciliata* .. .. nat. size



G. H. Robinson, Phot.

Nat. Size, x 2, 100, and 500.

CINTRACTIA EXSERTA.

PLATE XXXIX.

(*All Figures* × 500 *unless otherwise stated.*)

CINTRACTIA SORGHI-VULGARIS.

Fig.

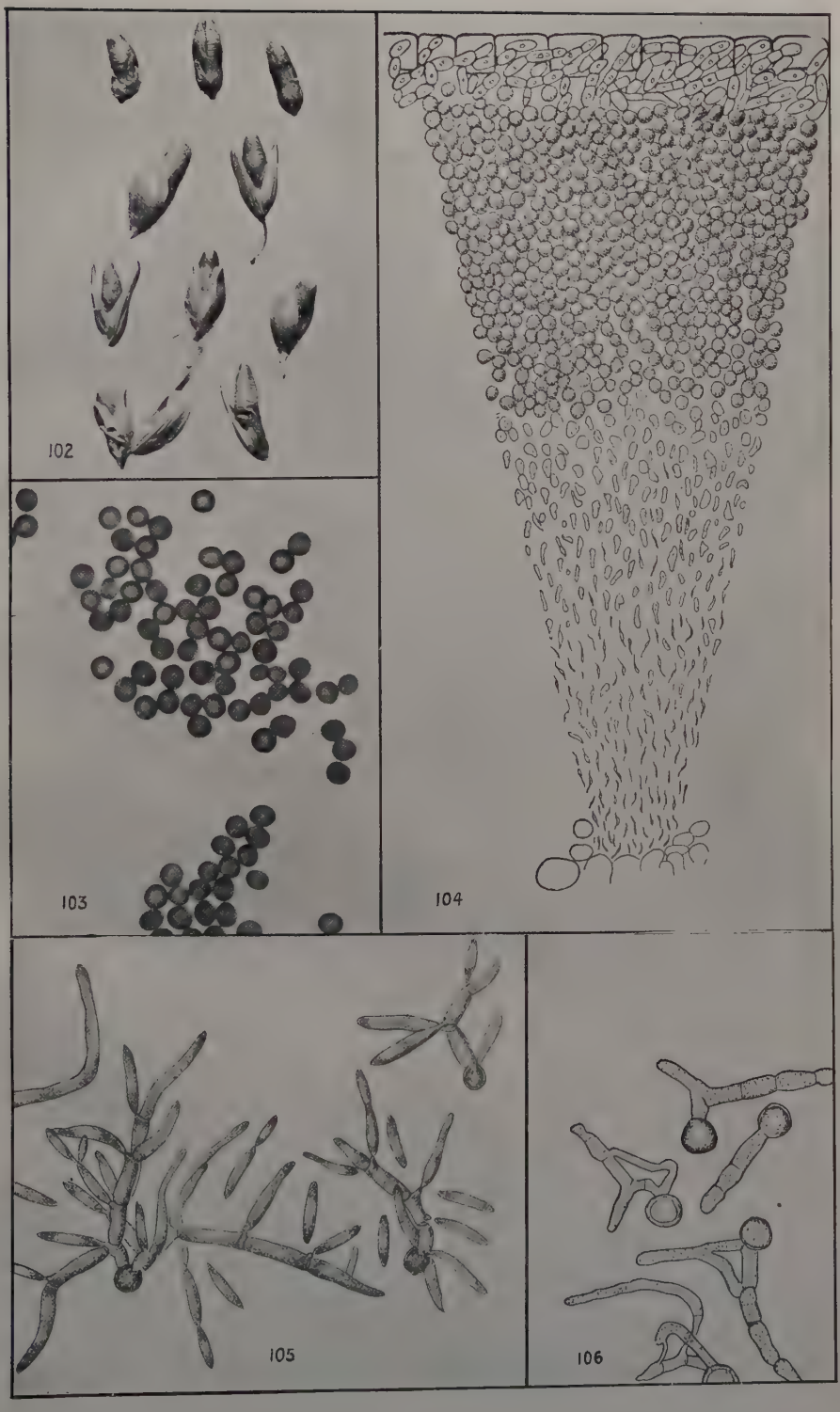
102. Diseased grains of *Andropogon sorghum*, showing distortion produced by *C. sorghi-vulgaris* .. .. × 2

103. Spores from same.

104. Cross section through base of a rather young infected grain. Small portion of columella is represented at the base, then immature spores passing gradually into the mature, and at the top the false membrane composed of epidermal cells and sterile fungus threads (after Clinton) .. .. .. × 250

105. Germination of spores in nutritive solution in different stages (after Brefeld) × 350

106. Germination of spores after 24 hours in water (after Norton).. .. × 600



G. H. Robinson, Phot.

x 2, 250, 350, 500, and 600.

CINTRACTIA SORGHI-VULGARIS.

PLATE XL.

(*All Figures* × 500 *unless otherwise stated.*)

SOROSPORIUM.

Fig.

107. Spore-ball of *S. enteromorphum* .. .. × 250

108. Spores of same.

109. Spore-balls of *S. cryptum* .. .. × 250

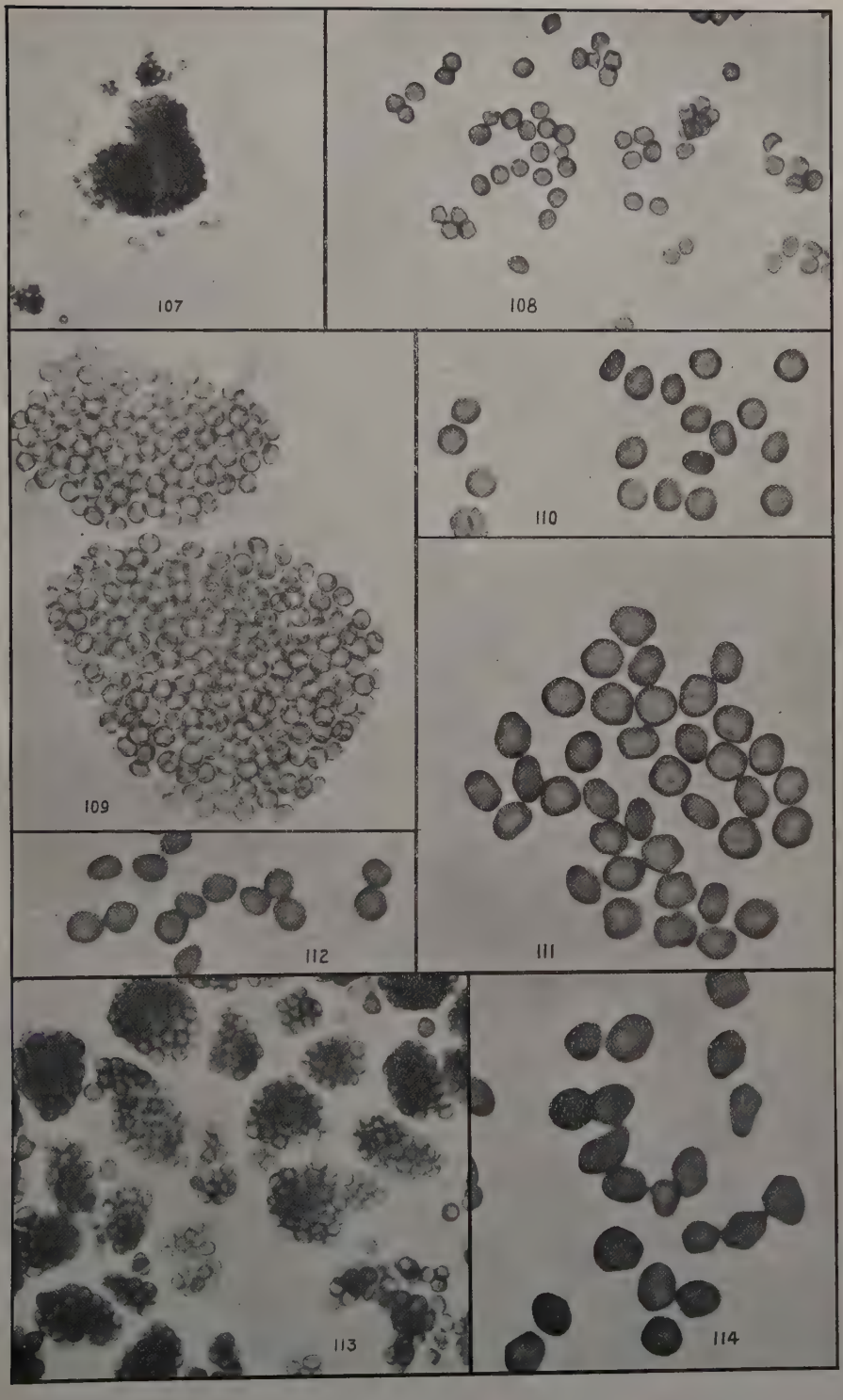
110. Spores of same, from *Panicum bicolor*, showing finely-warted surface.

111. Spores of same, sectional view.

112. Spores of same from *Panicum effusum*.

113. Spore-balls of *S. panici-miliacei* from *Chamaeraphis spinescens* .. × 200

114. Spores of same.



G. H. Robinson, Phot.

× 200, 250, and 500.

SOROSPORIUM.

PLATE XLI.

(All Figures × 500 *unless otherwise stated.*

SOROSPORIUM.

Fig.

115. Spore-balls of *S. consanguineum* from *Aristida behriana* .. .. × 250

116. Spores of same.

117. Spore-balls of *S. eriachnes* .. .. × 250

118. Spores of same, with one large lemon-coloured smooth cell.

119. Spore-balls of *S. mixtum* from Eriochloa .. .. × 250

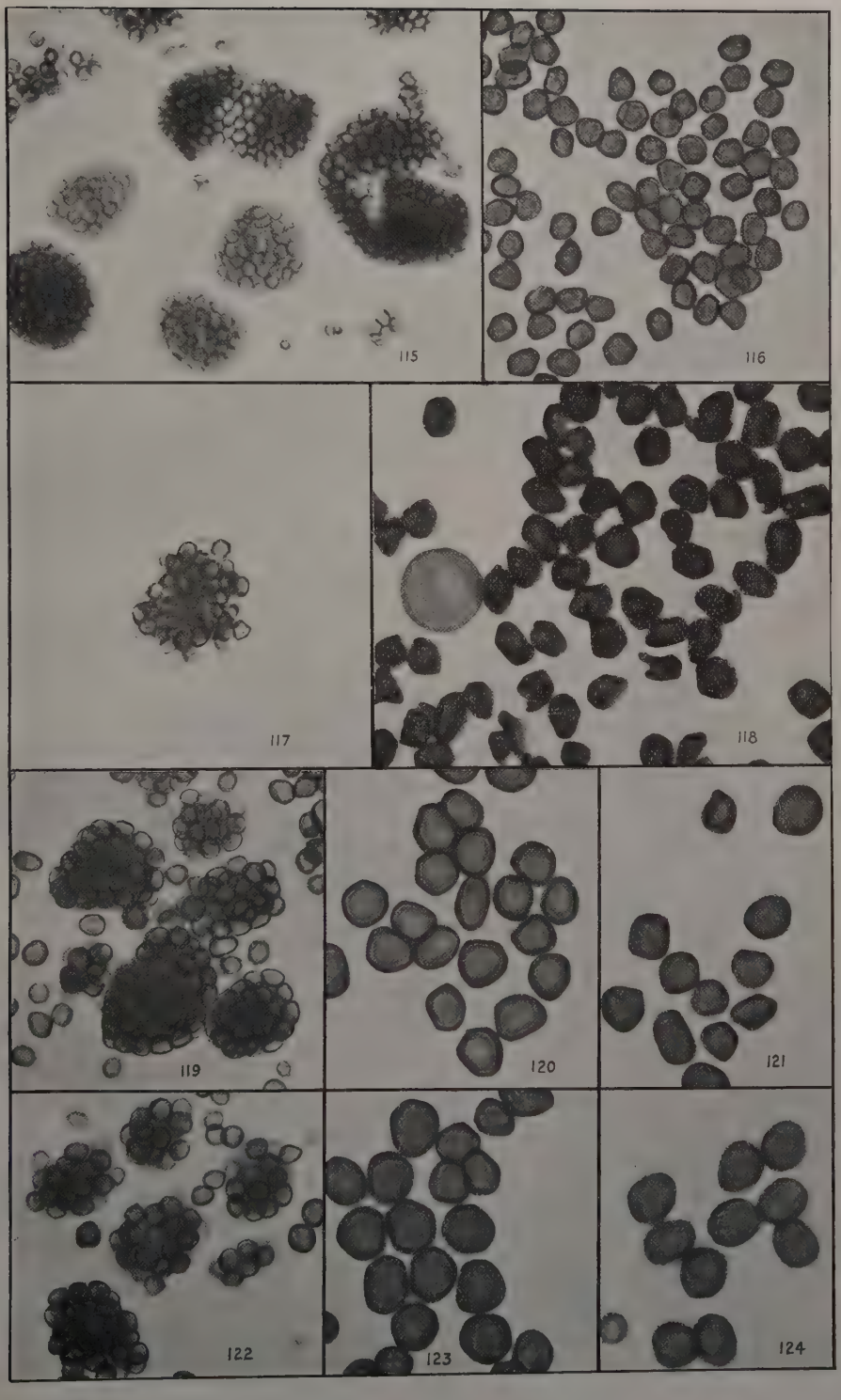
120. Spores of same, sectional view.

121. Spores of same, surface view showing warts.

122. Spore-balls of *S. mixtum* from Massee's type material of *Tilletia mixta* on Eriochloa .. .. × 250

123. Spores of same, sectional view.

124. Spores of same, surface view showing warts.



G. H. Robinson, Phot.

× 250 and 500.

SOROSPORIUM.

PLATE XLII.

(*All Figures* × 500 *unless otherwise stated.*)

SOROSPORIUM PILULIFORMIS.

Fig.

125. Section through ovary of *Juncus planifolius* affected with *S. piluliformis* × 50

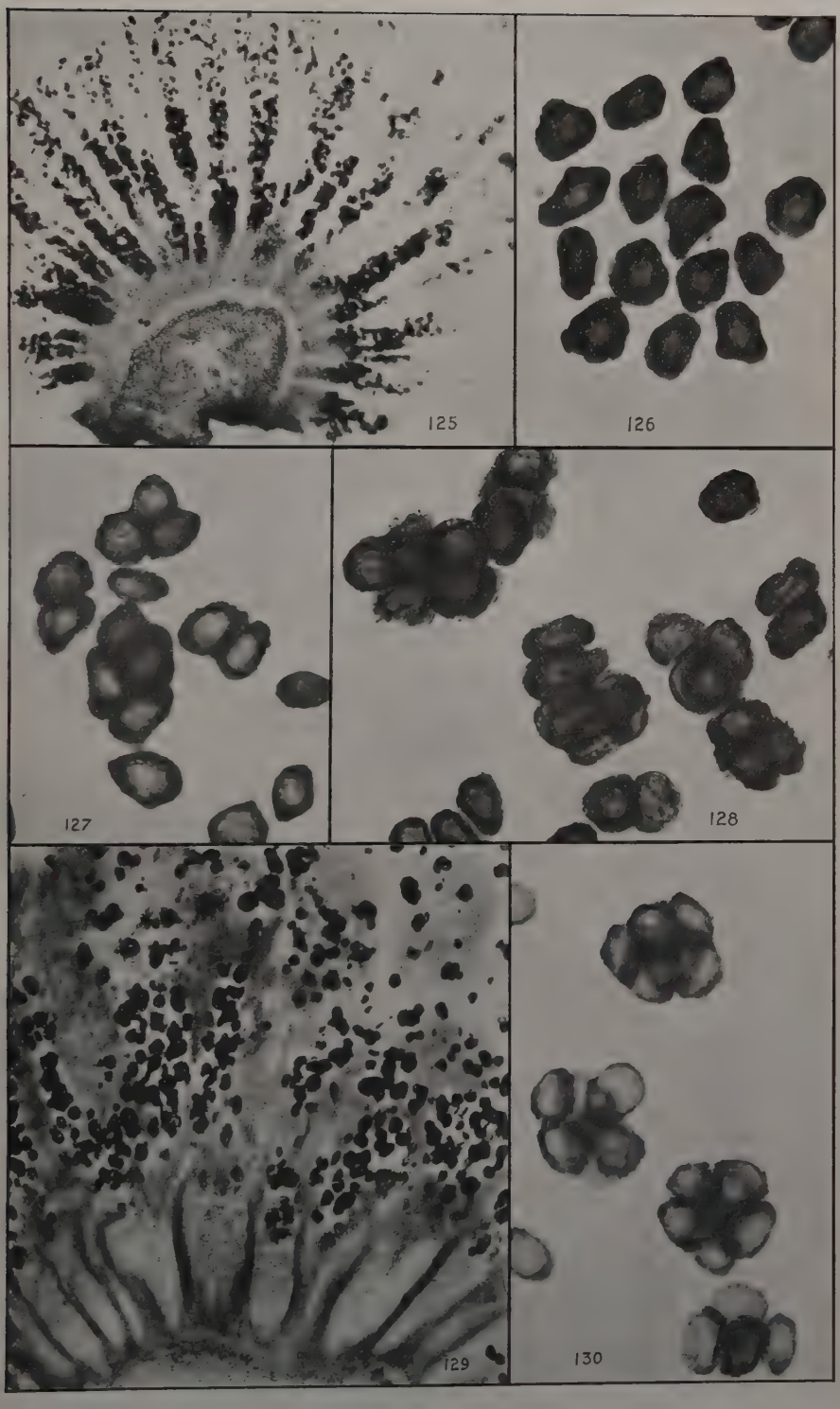
126. Isolated spores of *S. piluliformis*, labelled as *U. marmorata* in National Herbarium.

127. Spore-balls and isolated spores from *Juncus planifolius*.

128. Spore-balls of *S. piluliformis*, labelled as *U. marmorata* in National Herbarium.

129. Section through ovary of *Juncus planifolius* from Tasmania, affected with *S. piluliformis*, showing production of spore-balls .. .. .. × 150

130. Spore-balls of same.



G. H. Robinson, Phot.

x 50, 150, and 500.

SOROSPORIUM PILULIFORMIS.

PLATE XLIII.

(*All Figures* × 500 *unless otherwise stated.*)

SOROSPORIUM SOLIDUM.

Fig.

131. Inflorescence of *Schoenus imberbis* affected with *S. solidum* .. .. × 2

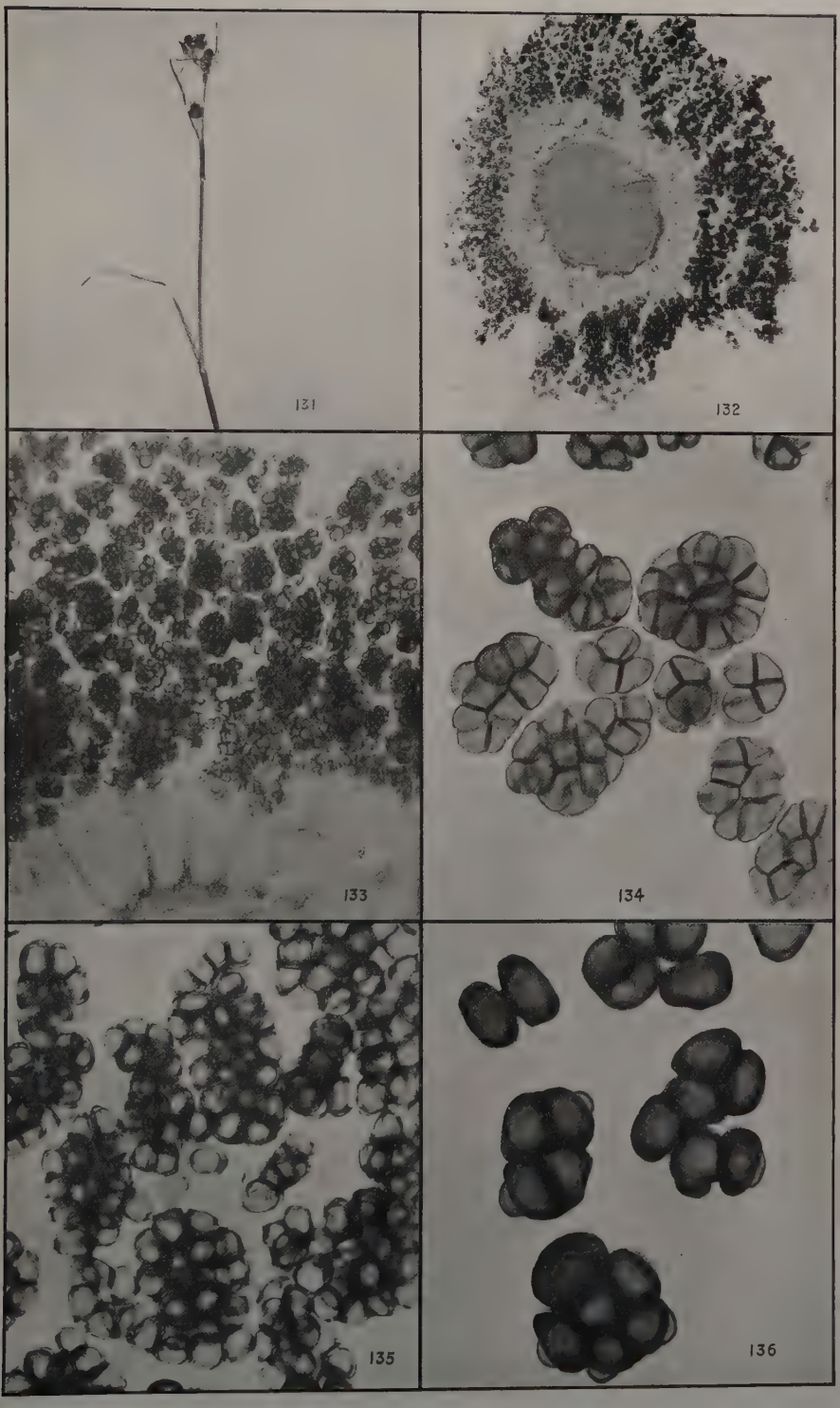
132. Section through ovary affected with same .. .. .. × 25

133. Portion of same enlarged .. .. × 100

134. Young spore-balls of same treated with caustic potash .. .. × 250

135. Mature spore-balls .. .. × 250

136. Spore-balls partially broken up, showing the so-called, sterile cells.



G. H. Robinson, Phot.

× 2. 25, 100, 250, and 500.

SOROSPORIUM SOLIDUM.

PLATE XLIV.

(*All Figures* × 500 *unless otherwise stated.*)

SOROSPORIUM.

Fig.

137. Spore-balls of *S. paspali* .. .. × 250

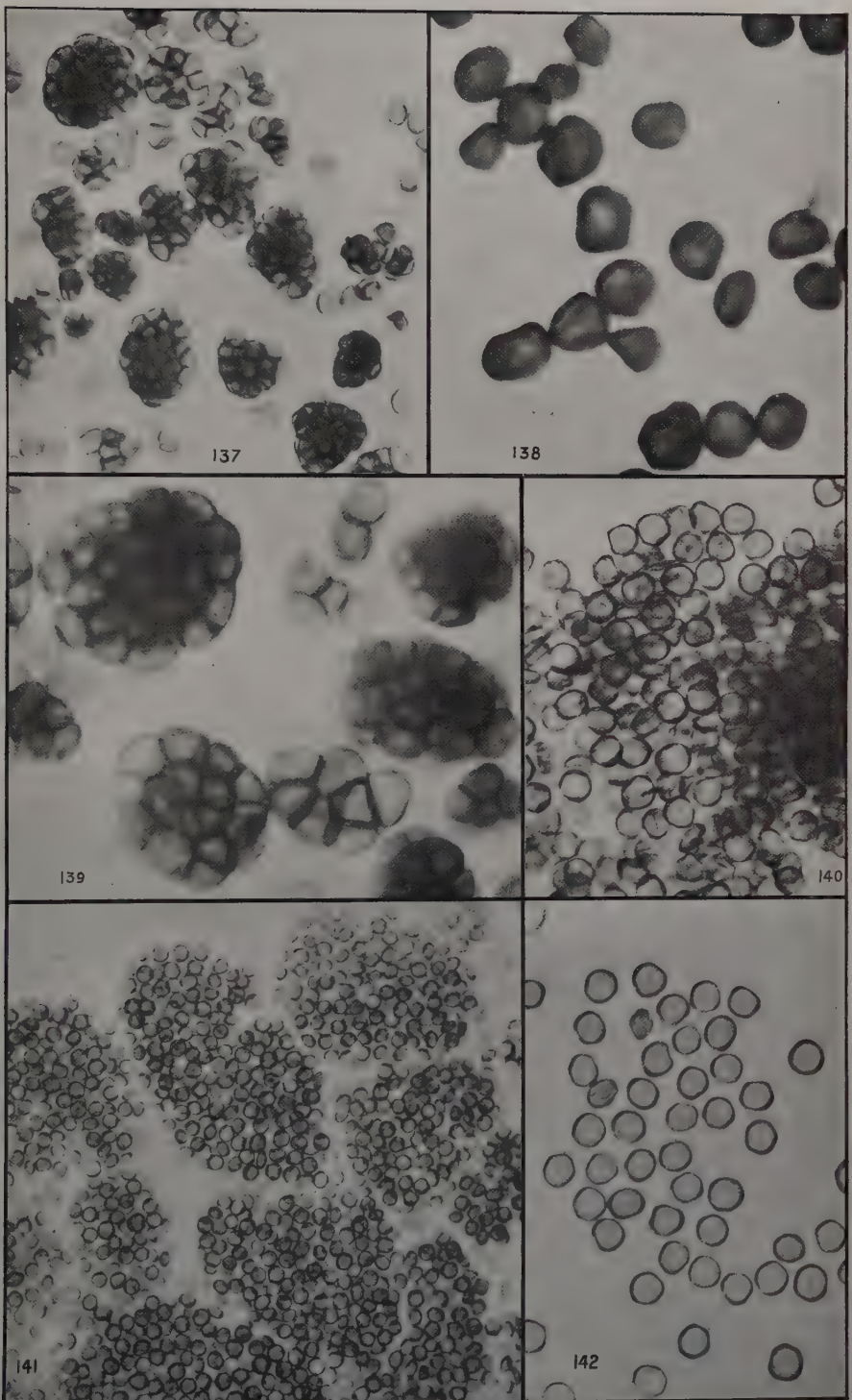
138 Spores of same.

139. Spore-balls of same.

140. Spore-ball of *S. turneri* disintegrating.

141. Spore-balls of same .. .. × 250

142. Spores of same.



G. H. Robinson, Phot.

x 250 and 500.

SOROSPORIUM.

PLATE XLV.

(*All Figures* × 500 *unless otherwise stated.*)

TOLYPOSPORIUM AND THECAPHORA.

Fig.

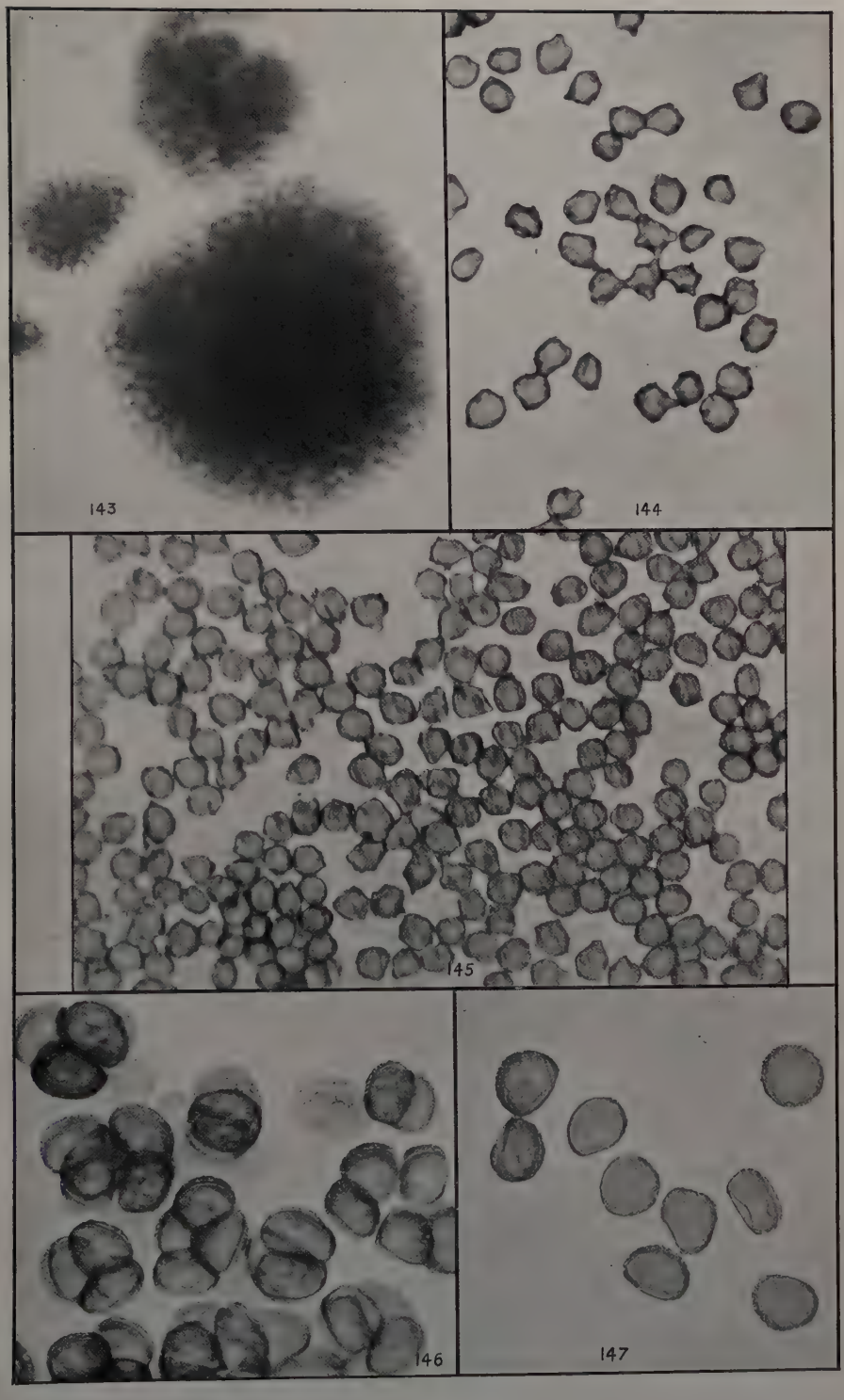
143. Spore-balls of *Tolyposporium globuligerum* .. .. × 250

144, 145. Spores of same.

146. Spore-balls of *Thecaphora lagenophorae.*

147. Individual spores of same.

NOTE.—Tolyposporium should be added to the title of the Plate.



G. H. Robinson, Phot.

× 250 and 500.

THECAPHORA.

PLATE XLVI.

(*All Figures* × 500 *unless otherwise stated.*)

TOLYPOSPORIUM.

Fig.

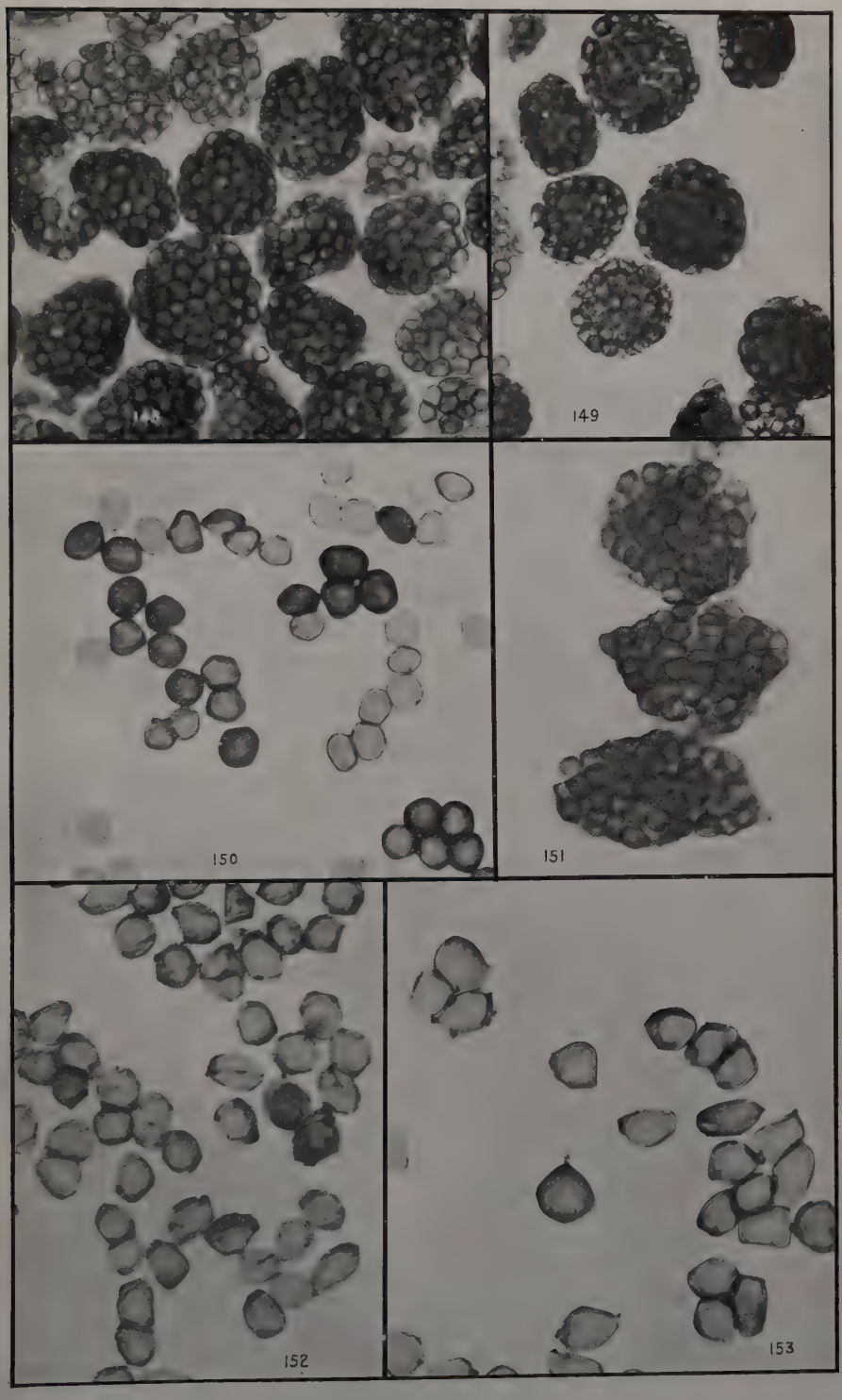
148. Spore-balls of *T. bursum* from Victoria ... ... × 250

149. Spore balls of *T. bursum* on *Anthistiria* from Queensland. Type material of *Ustilago bursa* Berk. in Bailey's Herbarium .. .. × 250

150. Spores of *T. bursum* from Victoria.

151. Spore-balls of *T. lepidoboli* .. .. × 250

152, 153. Individual spores of *T. lepidoboli.*



G. H. Robinson, Phot.

x 250 and 500.

TOLYPOSPORIUM.

PLATE XLVII.

(*All Figures* × 500 *unless otherwise stated.*)

TOLYPOSPORIUM.

Fig.

154. Spore-balls of *T. rodwayi* .. .. × 250

155. Spore-balls of *T. lepidospermae* .. .. × 250

156. Individual spores of same, showing thick-warted epispore.

157. Spore-balls of *T. muellerianum* .. .. × 250

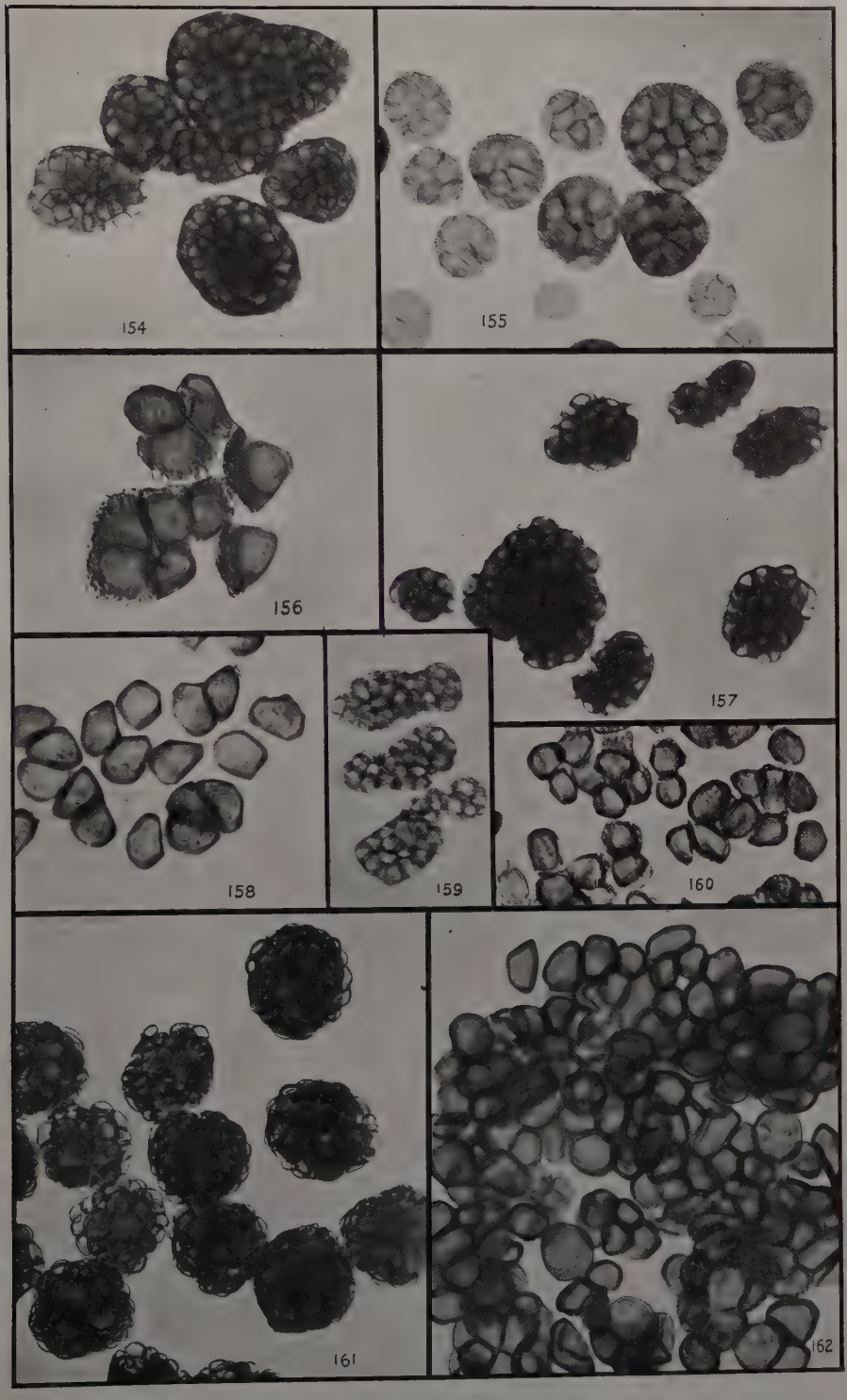
158. Spores of same.

159. Spore-balls of *T. junci* from Sydow's Ustilagineen, No. 373 .. .. × 250

160. Spores of same.

161. Spore-balls of *T. juncophilum* .. .. × 250

162. Spores of same.



G. H. Robinson, Phot.

x 250 and 500.

TOLYPOSPORIUM.

PLATE XLVIII.

(*All Figures* × 500 *unless otherwise stated.*)

TILLETIA.

Fig.

163. Spores of *T. levis.*

164, 165. Germinating spores of same.

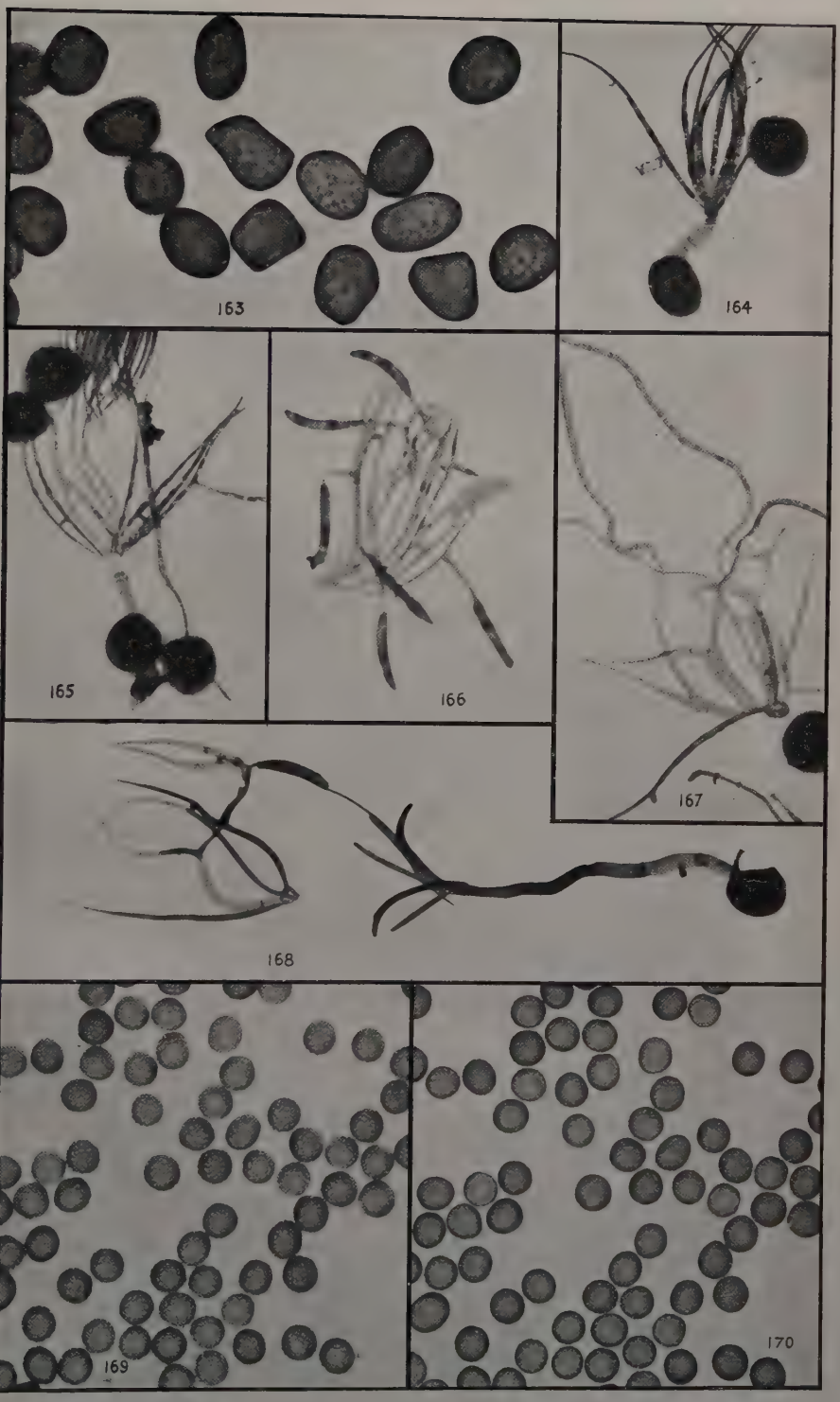
166. Conidia of same germinating and producing secondary sickle-shape conidia.

167. Coalesced conidia of same germinating and producing long threads.

168. Germinating spore of same with elongated septate promycelium and abnormally short conidia.

169. Spores of *T. tritici*, surface view .. .. × 250

170. Spores of same, sectional view .. .. × 250



G. H. Robinson, Phot. × 250 and 500.

TILLETIA.

PLATE XLIX.

(*All Figures* × 500 *unless otherwise stated.*

TILLETIA INOLENS.

Fig.

171. Spores of *T. inolens*, sectional view .. .. × 250

172, 173. Spores of same, surface view .. .. × 250

174. Surface view of spore of same, showing bead-like markings on ridge.

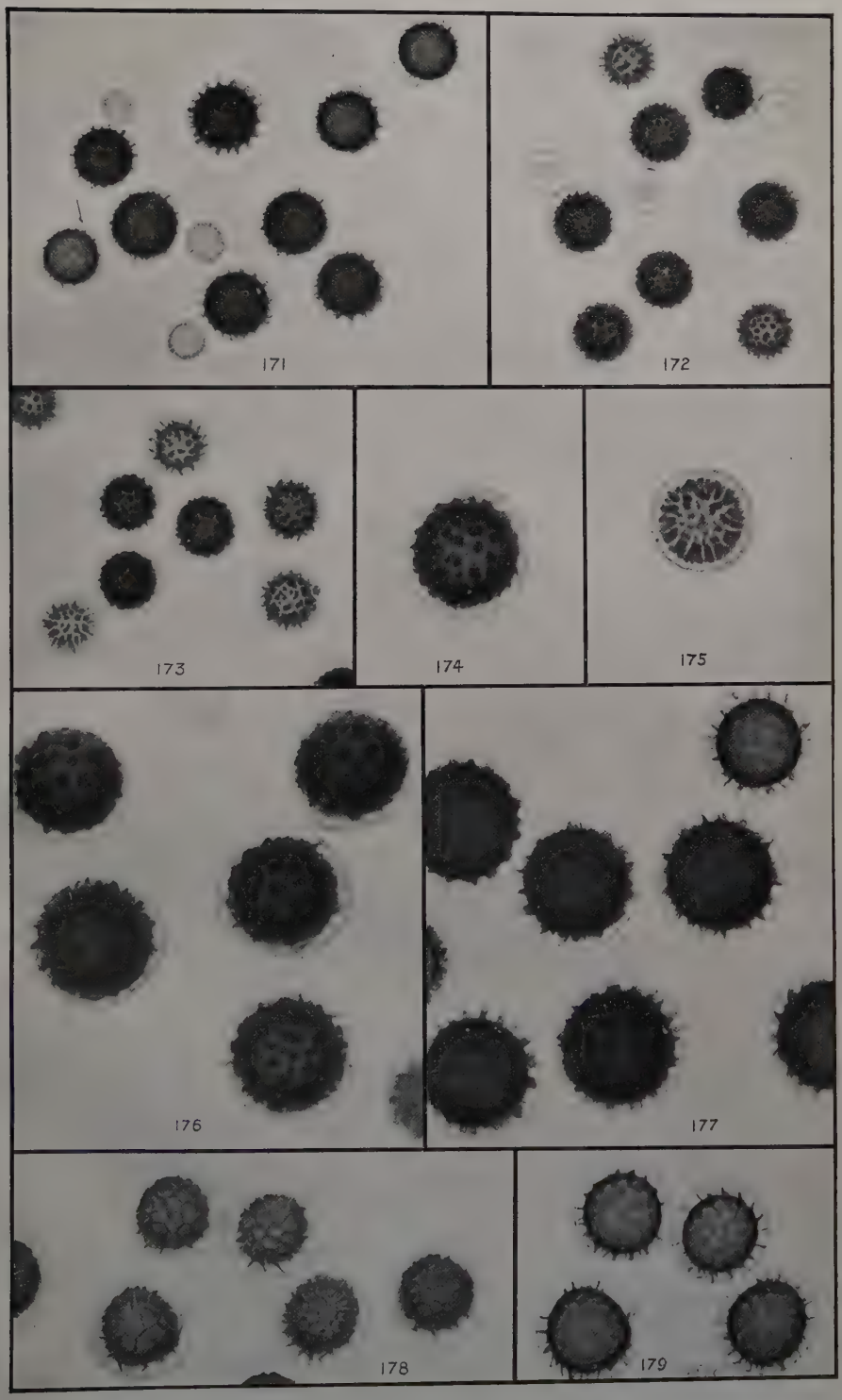
175. View of same, median between surface and sectional.

176. Surface view of same.

177. Sectional view of same.

178. Surface view of spores of *T. holci* from Sydow's Ustilagineen, Exs. 372.

179. Sectional view of same.



G. H. Robinson, Phot.

× 250 and 500.

TILLETIA INOLENS.

PLATE L.

(*All Figures* × 500 *unless otherwise stated.*)

TILLETIA AND ENTYLOMA.

Fig.

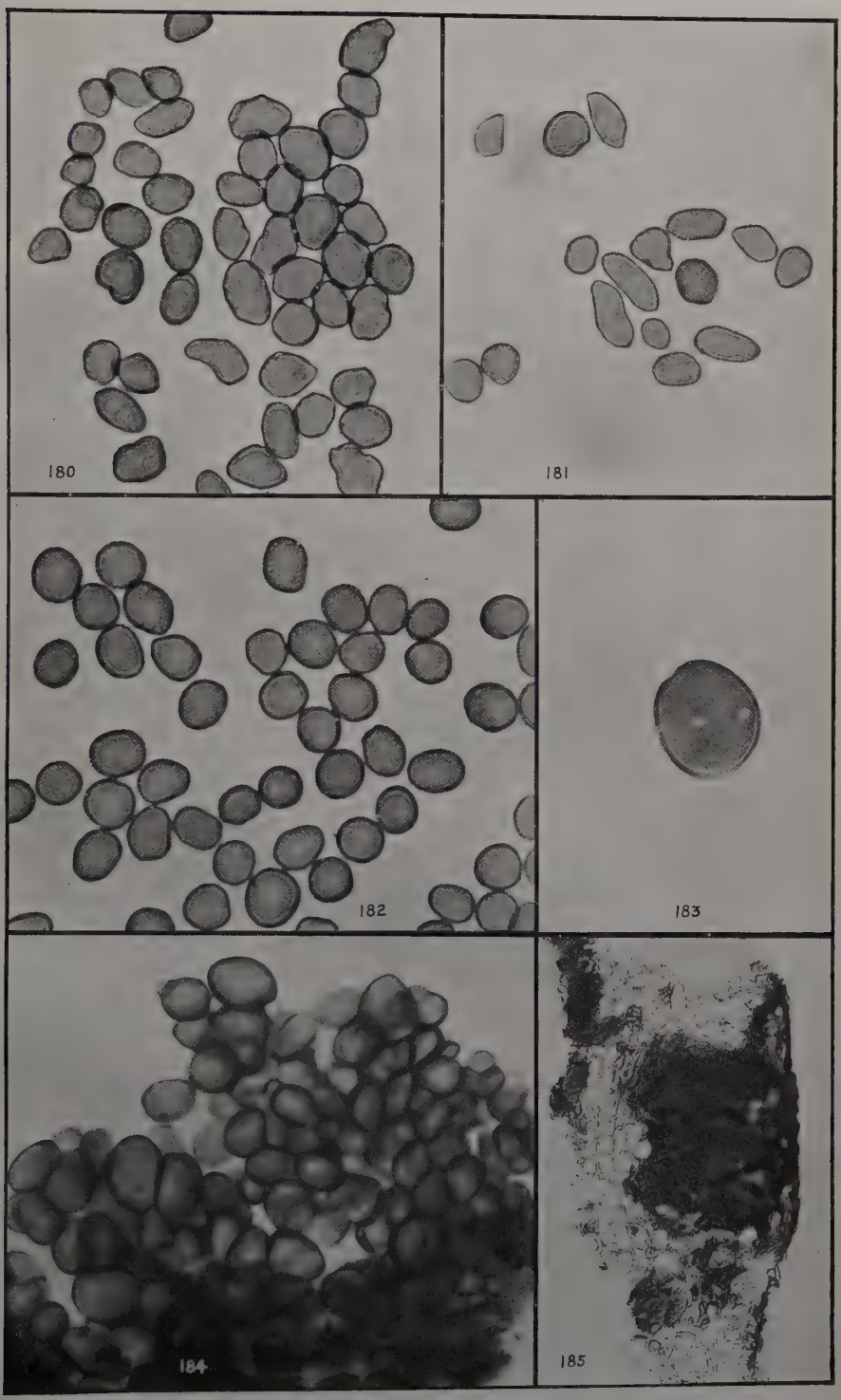
180, 181. Spores of *T. striaeformis* from Rye grass.

182. Spores of same from *Poa annua.*

183. Spore of so-called *T. epiphylla* Berk. on *Zea mays*, from type material, showing germ-pores, and proving it to be really a uredospore of *Puccinia maydis.*

184. Spores of *Entyloma eugeniarum.*

185. Section of leaf of *Eugenia* through sorus of same .. .. .. × 100



G. H. Robinson, Phot.

x 100 and 500.

TILLETIA AND ENTYLOMA.

PLATE LI.

(*All Figures* × 500 *unless otherwise stated.*)

UROCYSTIS.

Fig.

186. Section of wheat stem affected by *Urocystis tritici*, showing the cavities partially filled with spores .. .. × 20

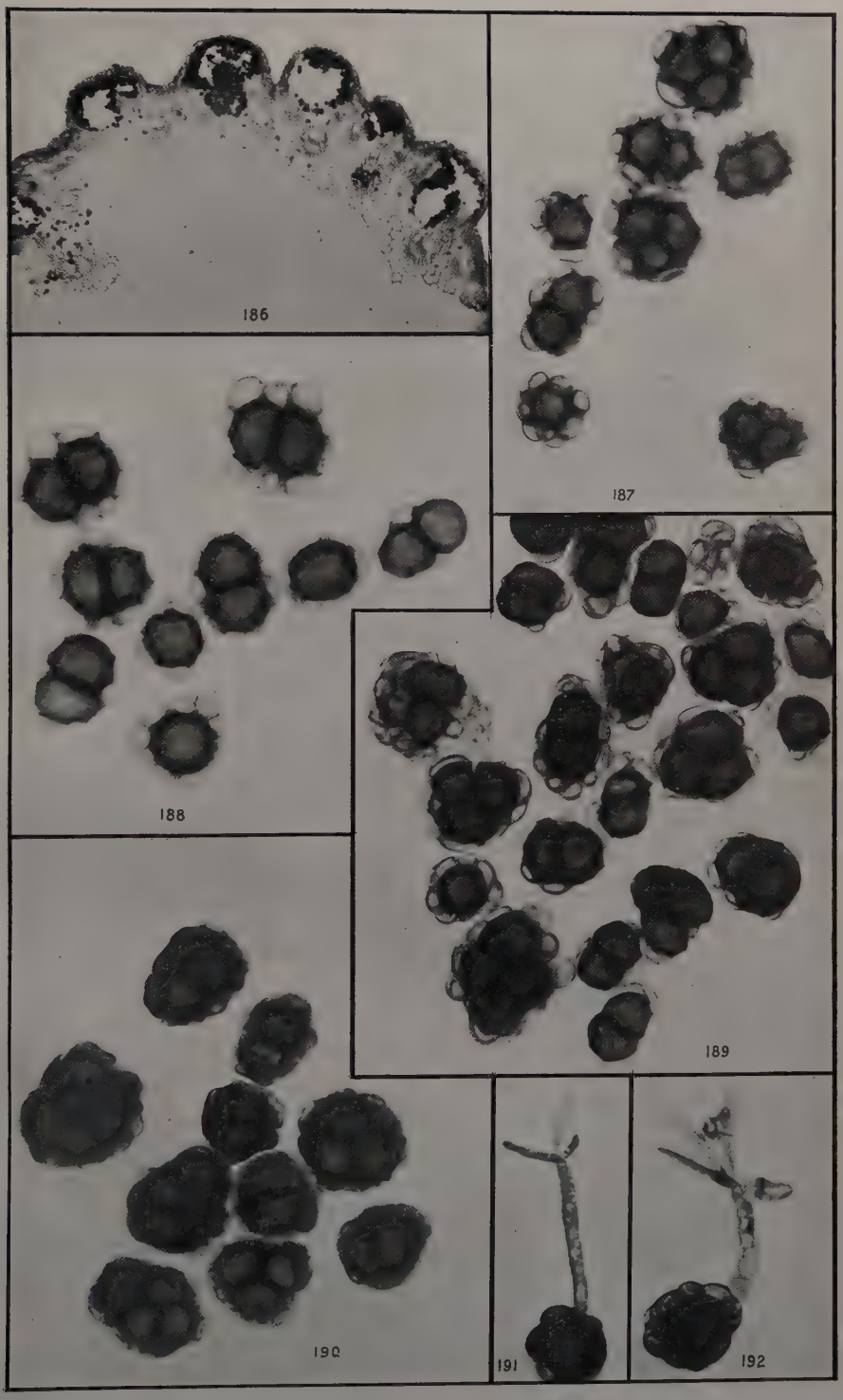
187. Spore-balls of *Urocystis occulta* from *Poa caespitosa*.

188. Spore-balls of *Urocystis tritici* from wheat.

189. Spore-balls of *Urocystis occulta* from Rye grown in Germany.

190. Spore-balls of *Urocystis stipae*.

191, 192. Germinating spores of *Urocystis tritici* from wheat.



G. H. Robinson, Phot.

x 20 and 500.

UROCYSTIS.

PLATE LII.

(*All Figures* × 500 *unless otherwise stated.*)

UROCYSTIS.

Fig.

193. Spore-balls of *Urocystis agropyri.*

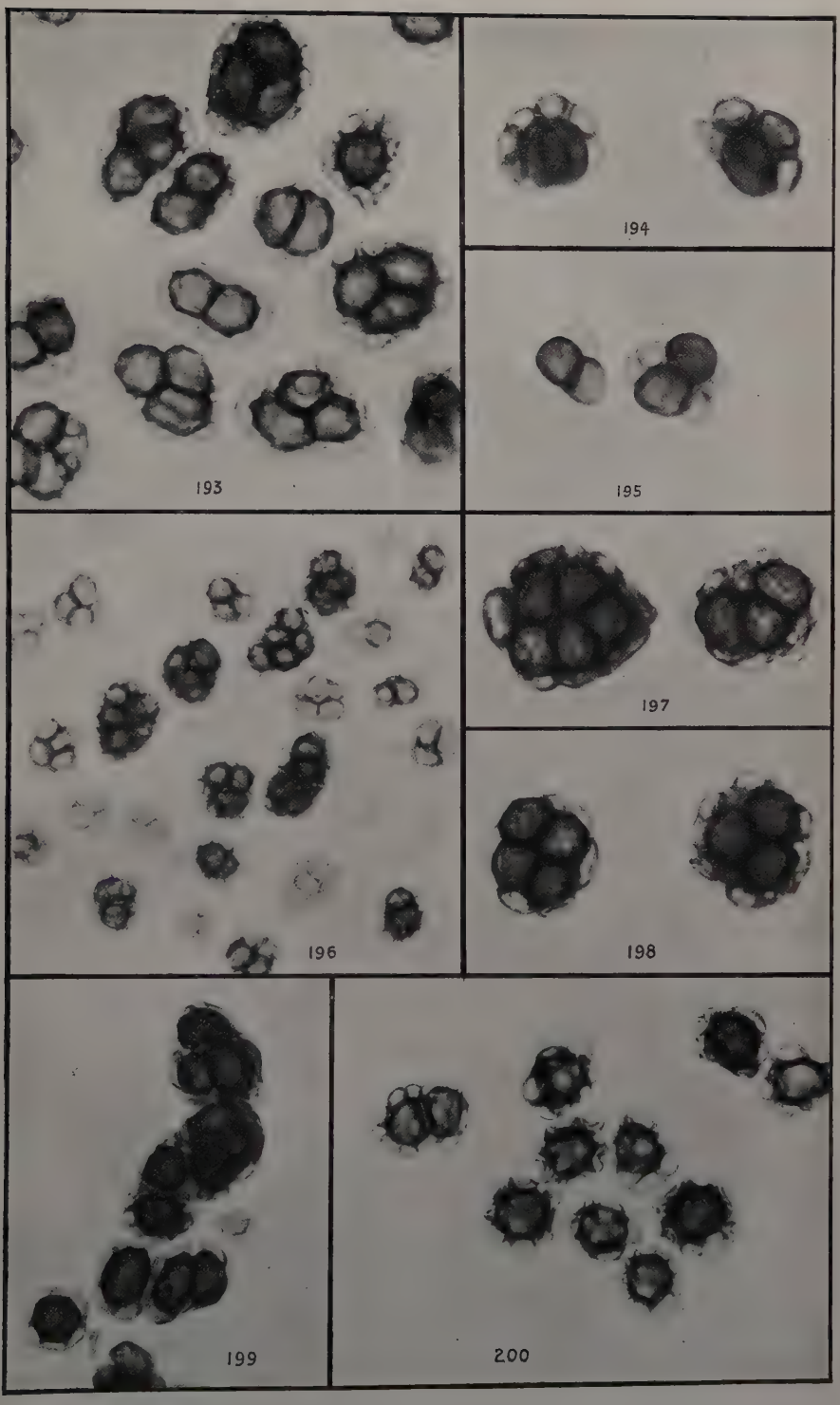
194, 195. Spore-balls of *Urocystis anemones.*

196. Spore-balls of *Urocystis hypoxidis* .. .. × 250

197, 198. Spore-balls of same.

199. Spore-balls of *Urocystis colchici* from Sydow's Ustilagineen, Exs. 246.

200. Spore-balls of *Urocystis destruens.*



G H. Robinson, Phot.

× 250 and 500.

UROCYSTIS.

PLATE LIV.

(*All Figures* × 500 *unless otherwise stated.*)

SOROSPORIUM TUMEFACIENS.

Fig.

210. Smutted and sound heads of *Stipa pubescens* R. Br. .. .. nat. size

211. Cross-section of inflorescence showing vascular bundles surrounded by spore-balls .. .. × 4

212. Spore-balls .. .. × 250

213. Spores.

214. Spore germinating in water, and showing septate branching promycelium bearing lateral and terminal conidia.

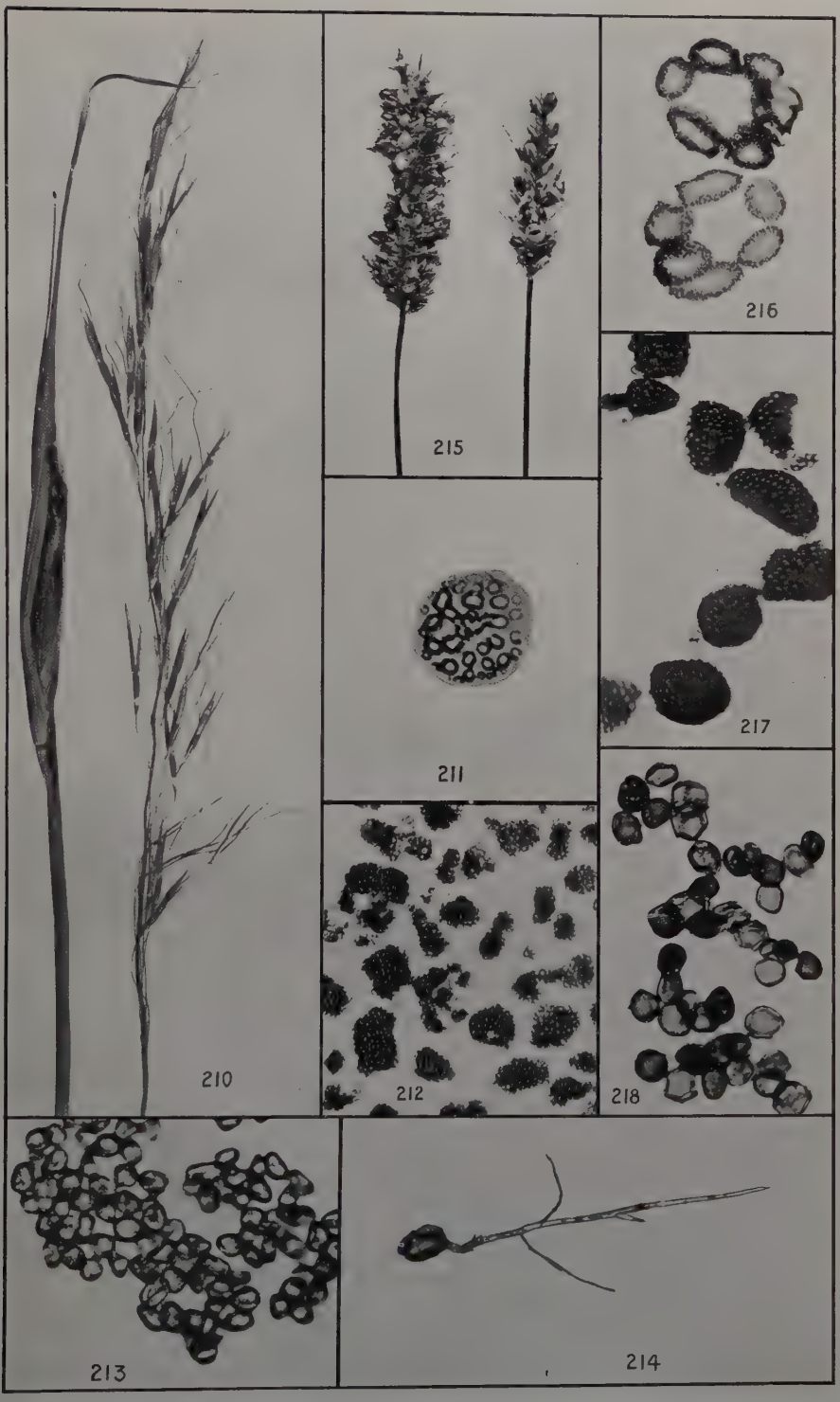
SOROSPORIUM SETARIAE.

215. Smutted and partially smutted heads of *Setaria glauca* Beauv. .. nat. size

216. Cross-section of inflorescence, showing spore-balls around vascular bundles × 12

217. Spore-balls .. .. × 250

218. Spores.



C. C. Brittlebank, Phot.

Nat. Size, × 4, 12, 250, 500.

SOROSPORIUM.

PLATE LV.

(*All Figures* × 500 *unless otherwise stated.*)

TILLETIA FUSCA.

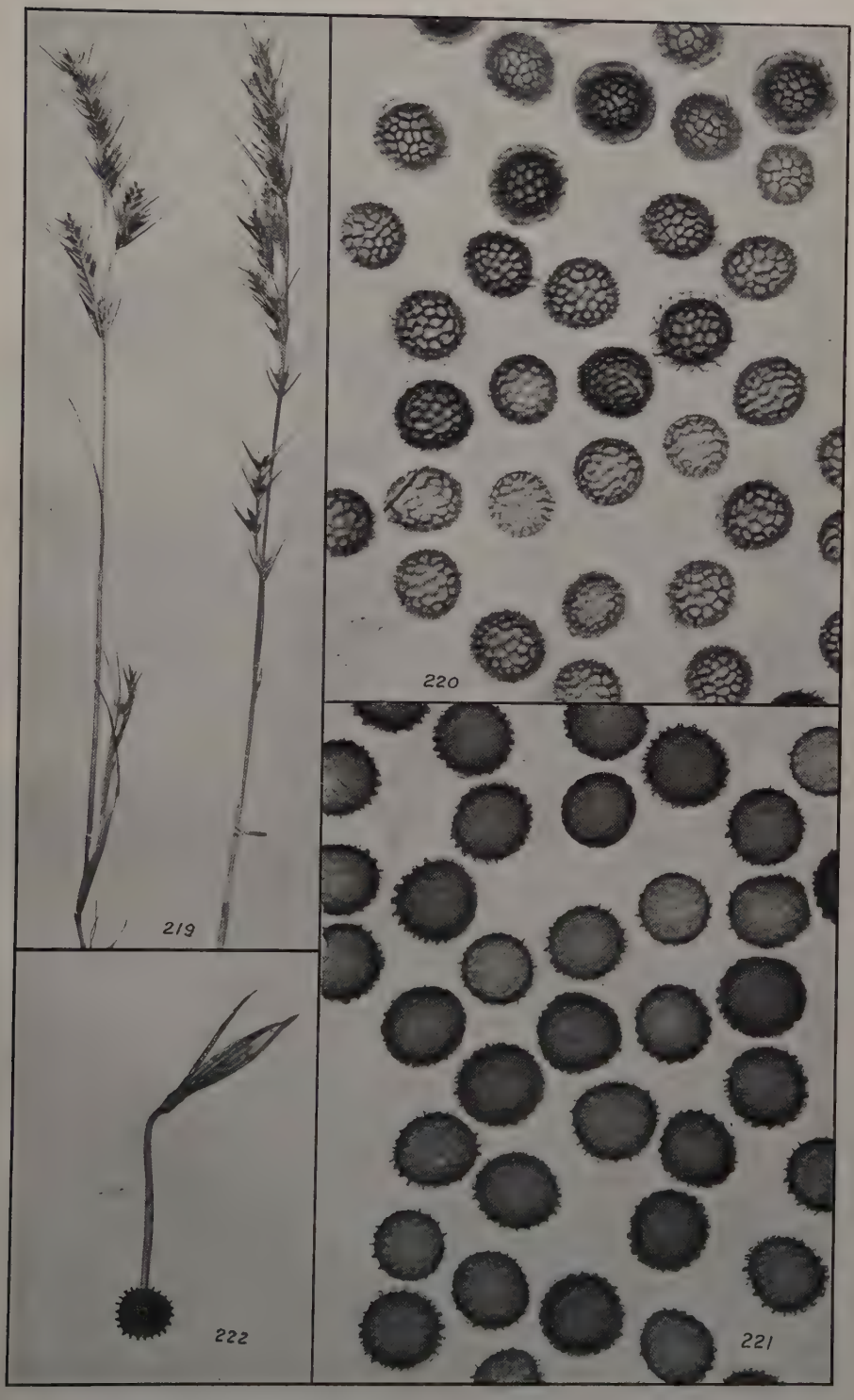
Fig.

219. *Festuca bromoides* with every spikelet smutted .. .. .. nat. size

220. Spores of the same in surface view, showing raised ridges and gelatinous envelope.

221. Spores in optical section.

222. Spore germinating after 17 days in water on a slide, with elongated bi-septate promycelium bearing 7 conidia at its apex .. .. .. × 300



C. C. Brittlebank, Phot. Nat. Size, × 300, 500.

TILLETIA FUSCA.

PLATE LVI.

(*All Figures* × 500 *unless otherwise stated.*)

TILLETIA, ENTYLOMA, SOROSPORIUM, AND THECAPHORA.

Fig.

223. Barley grass, with *Tilletia hordei* concealed by the glumes; glumes removed on one side showing smut-balls .. .. nat. size

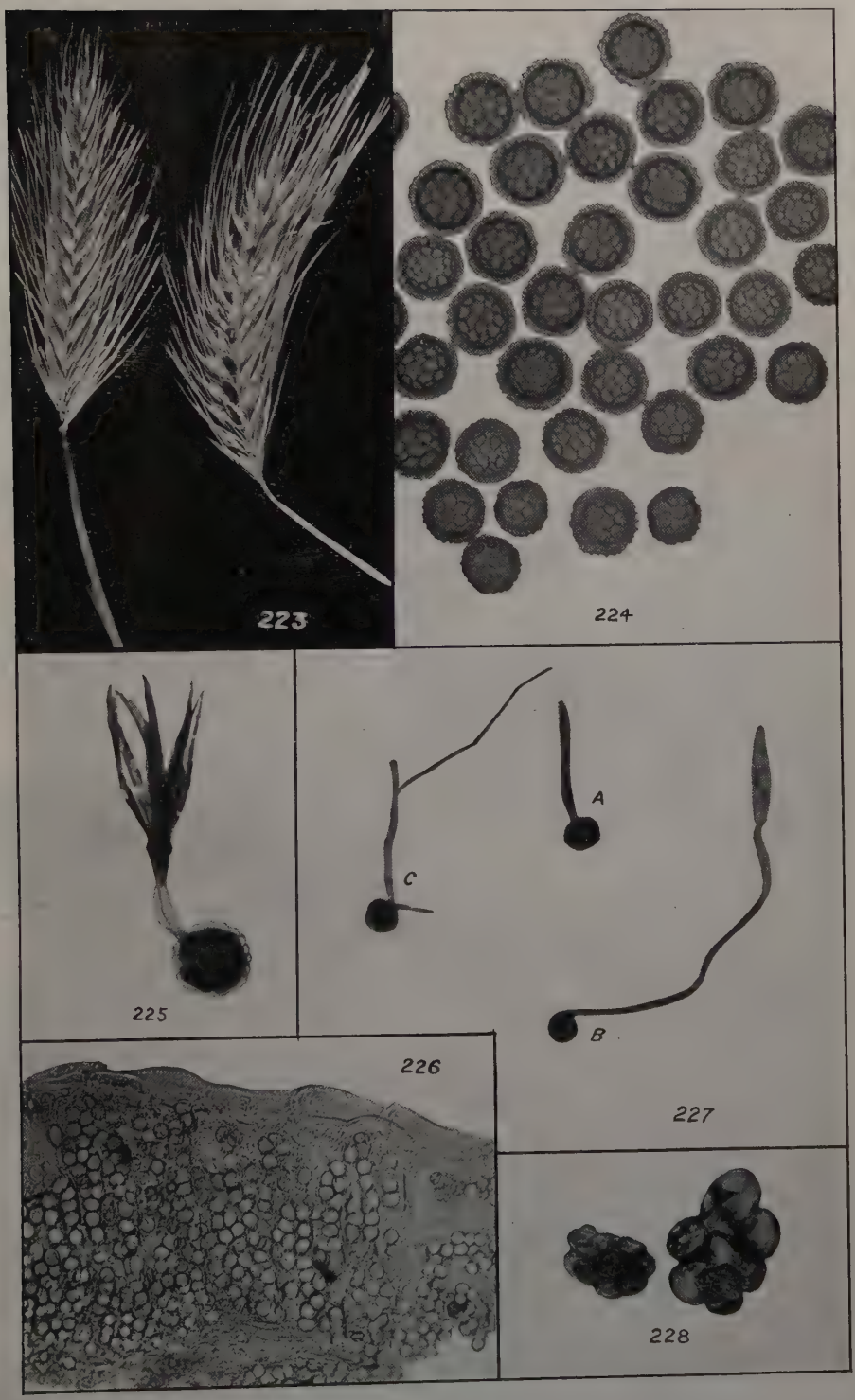
224. Spores in surface view, showing net-like markings and gelatinous envelope.

225. Spore germinating after 24 days in water, with one septate promycelium bearing 7 conidia at its apex .. .. × 300

226. Section through leaf of *Melilotus indica*, showing the spores of *Entyloma meliloti* largely replacing the ordinary tissues .. .. × 170

227. Spores of *Sorosporium cryptum* germinating after 41 hours floating on water. A—Non-septate promycelium only; B—Elongated non-septate promycelium bearing a single stout 2-septate conidium at apex; C—Septate promycelium with lateral and terminal conidia, the terminal conidium giving off at the side a slender septate germ-tube.

228. Two spore-balls of *Thecaphora leptocarpi* .. .. × 250



C. C. Brittlebank, Phot.

Nat. Size, x 170, 300, 500.

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Note 1.—Page 155. The discovery of the smut on *Cynodon dactylon* Pers. in Victoria on 31st March, 1910, has rendered it necessary to add to the localities for *Ustilago cynodontis* P. Henn. the following:—Victoria—On Roadside near Melbourne, March, 1910 (Brittlebank).

Note 2.—Page 64. This adds another Ustilago to Victoria, and a Tolyposporium has also to be added, as well as a Tilletia to New South Wales, so that the total number of species in each of these States will be—Victoria 46, and New South Wales 23.

WORKS BY D. McALPINE.

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OF

The Rusts of Australia : their Structure, Nature, and Classification.

BY D. McALPINE.

Professor J. C. Arthur, in *Journal of Mycology*, March, 1907.

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Preceding the systematic part the first twenty chapters are devoted to a discussion of the general subject of rusts in its various aspects, and from the most modern point of view. It is by much the best account now available in the English language.

The thoroughness with which the author has accomplished his task, the culmination of many years of observation and study, has insured a valuable work of reference for both local and other botanists. But even more than this, the broad spirit in which the work has been conceived and the ability shown to discover and interpret the less obvious morphological structures, give added value to the record of facts.

It is this clear insight, and the accuracy and fulness of details, that commend the work to all students of the rusts in every part of the world.

Professor C. E. Bessey in *Science*, January, 1907.

Part I., consisting of 75 pages, is devoted to the general characters and mode of life of the rusts. This portion would be a very helpful text-book for college students anywhere, since the matter is presented in a clear and comprehensive manner. Fifty-five plates (eleven of them beautifully and accurately coloured) help to render the descriptions more easily understood. A glossary of technical terms, a bibliography, an alphabetical host index, a fungus index (alphabetical by genera), and a general index, complete this satisfactory volume.

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I am convinced that your beautiful work, by its contents as well as by its excellent illustrations, will meet with general recognition, and I trust that it may give a strong impetus to the further investigation of the flora of your interesting country.

The letterpress of your book has given me much information, and it has been of great interest to me to receive a complete account of the rust-flora of Australia.

Professor Saccardo, author of *Sylloge Fungorum*, 18 vols.

This magnificent volume, containing a monograph of the Uredines of Australia. It is very important, executed with great care and exceedingly well illustrated. The preliminary and general part of it is very clear and instructive.

Revues Générale des Sciences pures et appliquées, 30th August, 1907.

The requirements of agriculture, which constitutes one of the leading sources of wealth for the Australian colonies, have necessitated, for a long time, the creation in the States of Departments of Agriculture, among which that of the State of Victoria is distinguished by the indefatigable zeal which it displays in defence of the interests with which it is charged.

The Department of Agriculture has obtained from one of the savants attached it—Mr. McAlpine—a study as complete as possible of the various rusts which occur in Australia. The work, in which all these observations are recorded and illustrated with numerous plates, some of which are beautifully coloured, reflects great credit on the author and on the Department of Agriculture of Victoria.

The Times, Weekly Edition Supplement, 24th May, 1907.

In its own particular sphere the book is highly instructive, and will be appreciated by students of agricultural science and welcomed by suffering farmers as furnishing a solid groundwork for the carrying out of experiments with preventive or remedial treatment. The extent to which agricultural pursuits in Australia are hampered and injured by rust is very great, and no more important work could be undertaken than that to which Mr. McAlpine is devoting his attention.

The Journal of Botany, August, 1906.

He has earned the thanks of all plant-growers in Australia by this useful and interesting account of rust-fungi. It remains with the grower himself to take advantage of the knowledge offered, and to carry into practice the author's suggestions and recommendations.

The Victorian Naturalist, August, 1906.

By patient work during a period of fifteen years, since the date of his first article on the subject, Mr. McAlpine seems to have at last conquered many of the mysteries in the growth and occurrence of these insidious pests, and has now arranged them in such a way, and with such copious notes and references, that future workers have a good foundation on which to base their observations.

The Age, Melbourne, 25th May, 1906.

Altogether, the volume will be a welcome addition to the botanical literature of Australia, and should prove of immense assistance in future to those engaged in the problem of the prevention or of the mitigation of disease.

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